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Estación Biológica Doñana CSIC
Department of Ethology and Biodiversity Conservation

ULL Universidad de La Laguna

MINISTERIO DE ECONOMÍA, INDUSTRIA Y COMPETITIVIDAD

Evolutionary responses to the independent and interacting action of sexual selection and population spatial structure: Insights from experimental evolution in a species with sexual conflict

Thesis supervisor: Francisco García González

Academic tutor: Mariano Hernández Ferrer

This thesis is presented by Eduardo Rodríguez Expósito, BSc (Hons) and MSc in Biology, for the degree of Doctor of Philosophy of The University of La Laguna

San Cristóbal de La Laguna

2018

Signed:

Eduardo Rodríguez Expósito

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Dr. Francisco García González, Senior Researcher (Científico Titular) at Doñana Biological Station (Spanish Research Council, CSIC) and Prof. Mariano Hernández Ferrer, Professor of Genetics at the University of La Laguna (ULL), in their role as Thesis Director and Academic Tutor of Eduardo Rodríguez Expósito

CERTIFY

That the present thesis entitled "*Evolutionary responses to the independent and interacting action of sexual selection and population spatial structure: Insights from experimental evolution in a species with sexual conflict*" contains original research that is of enough quality to be presented by the graduate student Eduardo Rodríguez Expósito (BSc (Hons.) and MSc in Biology), in the presence of the designated examining board, to aim to obtain the degree of Doctor of Philosophy from the University of La Laguna.

La Laguna, 25th May 2018.

Signed:

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Francisco García González

Academic tutor:
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"Scientists have become the bearers of the torch of discovery in our quest for knowledge."

Stephen Hawking

"Science is not only a disciple of reason but, also, one of romance and passion."

Stephen Hawking

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To my family.

Specially to my mother and grandmother.

Wherever you are now, I hope you are proud of me.

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Acknowledgements (Agradecimientos)

Despite the remaining parts of this document are written in English, I do believe I should write this section in my mother tongue, to be completely sure I can clearly express my feelings at this moment.

Pese a que la tesis esté escrita en inglés, creo que esta sección debo escribirla en la lengua que mejor domino, para asegurarme de que expreso con claridad lo que siento en este momento.

En primer lugar, a mi familia. Por creer en mí ciegamente, sin atisbo de duda alguna. Por su constancia en el apoyo aún desde la distancia. Por el amor recibido cada uno de los días que he permanecido lejos de ustedes y por el calor de un hogar que me esperaba con los brazos abiertos cada vez que volvía casa. A mi padres, Ventura y Berta, por ser unos referentes de los que todo hijo se puede sentir orgulloso. A ti mamá, por inculcarme los mejores valores, que me han permitido llegar a donde he llegado: sacrificio, constancia, dedicación, pero sobre todo, por enseñarme a entregarme por completo a todo aquello que me apasiona. A ti papá, por el margen de tiempo que me diste, por llevar las riendas del hogar en mi ausencia, por cargar con todo el peso mientras yo seguía luchando por alcanzar este objetivo. A mi hermano Carlos, por su cariño y el apoyo incondicional que ha supuesto para mí durante estos cuatro años. Porque al mirar a mi lado siempre estás ahí. A mi futura esposa, Estefanía, por sacarme cada día una sonrisa por la mañana con sus mensajes, por estirar cada día hasta el último momento dándome señales del más puro de los amores y por hacer de mi vida la más maravillosa de las historias. A mi abuela Ina, mi abuela tata, por ser un faro en mi vida, por todas las lecciones que me enseñaste, por estar pendiente de mi desde el primer instante de mi vida hasta el final de tus días. A todos ellos, en especial a mi madre y mi abuela, perdón por el tiempo que no les pude dedicar estos años y gracias porque sin duda ustedes han sido la base sobre la que se sustenta mi persona y todo lo que soy. Que no les quepa duda de que, aún desde la distancia, no me olvidé ni un solo día de ustedes y he querido hacer todo lo que estuviese en mi mano para mantenerme cercano a la familia. Hoy resuena en mi mente una de las frases de mi abuelita: "Si no lo consigues hoy, mañana será otro día para intentarlo de nuevo". Abuela, ese día ha llegado, ese mañana es hoy.

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A mis supervisores de las estancias en el extranjero, Leigh Simmons (Australia) y Michal Polak (EEUU). Por abrirme las puertas de sus laboratorios y acogerme durante dos períodos que les aseguro que no olvidaré jamás en la vida. A mi tutor de la ULL, Mariano, porque contigo empezó mi andadura en la ciencia y te has

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mantenido al pie del cañón durante todo el camino. A los miembros de mi Comité de tesis, Lazslo, John y Judith, por haberme hecho un hueco en sus agendas y haberme dado puntos de vistas enriquecedores a lo largo de toda mi tesis. A todos ellos gracias por haber hecho posible lo que en un principio me parecía tan sólo un sueño.

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Por último, quiero dar gracias a todos aquellos otros que me han ayudado en alguna fase de mi tesis, gente como Renee, que me acogió en su casa en DownUnder, Susi (Susanne Zajitschek) por ayudarme a crecer como científico y por las cervezas que hemos podido compartir en España y algún otro punto de Europa. A Ana Carvajal, por tu ayuda y por los momentos en los que hablamos acerca del sentido de la vida. Gracias por el humor y alegría que hicieron muchísimo más divertido mi paso por los laboratorios de la EBD. Y a los estudiantes que me ayudaron con los experimentos durante sus estancias, Christian, Ryan, Matthew y Fergus. Por haber añadido vuestro granito de arena para que todo este trabajo finamente pudiera ver la luz.

A todos, por ser como han sido y desempeñar los papeles que han desempeñado, porque sin duda alguna, sin cada uno de ustedes el camino y la experiencia habrían sido totalmente diferentes y me habría perdido esta maravillosa aventura. A todos, simple y llanamente, gracias.

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General introduction

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To choose and to be chosen, those are the questions. Selection is at the base of the game of life. Since natural selection, nowadays a cornerstone of modern biology, was brought to light in Darwin's influential book "On the origins of species by means of natural selection , or the preservation of favoured races in the struggle for life" (Darwin 1859), the study of selection and its effects on biological evolution has been an ever-present objective of evolutionary biologists.

Sexual selection: let's start from the beginning

Reproduction is a fundamental process in sexually reproducing species. However, passing the genes to the next generation may not to be so easy as it could seem. In sexually reproducing organisms, this process implies not only the survival until sexual maturity but also finding members of the opposite sex and "persuading" them to copulate and produce offspring (Darwin 1871; Andersson 1994; Andersson and Simmons 2006). Sexual selection refers to the evolutionary process that favours the increase in frequency of genes, and phenotypes associated, that confer a reproductive advantage to the individuals regarding the competition for mates and gametes (Parker 1979; Andersson 1994; Garcia-Gonzalez 2011). Nowadays, sexual selection is widely accepted as one of the most potent forces driving the evolution of numerous behavioural, ecological and physiological traits involved in sexual interactions (Andersson 1994; Andersson and Simmons 2006), and a force that has critical implications for population viability and the probability of extinction (e.g. Jarzebowska and Radwan 2010; Price et al. 2010; Wade 2010; Almbro and Simmons 2014), and for additional evolutionary processes such as reproductive isolation and speciation (Hosken and Stockley 2004; Ritchie 2007; Eberhard 2010a, b; Maan and Seehausen 2011; Simmons 2014).

Expanding the limits: sexual selection beyond copulation

The scope of the studies regarding sexual selection has faced a remarkable expansion in the last decades due to important realizations. Darwin's initial approach (Darwin 1871) limited sexual selection to a series of mechanisms which occur before copulation takes place (pre-copulatory sexual selection). Males use to compete with rivals for the access to potential mates and females use to choose a mating partner among the available mates based on certain traits that may reflect male's quality (Andersson 1994). This point of view was based on the assumption that females are generally monogamous. However, the ground-breaking work of Geoff Parker in the 1970's showed that sexual selection continues after mating (Parker 1970a, b; Boorman and Parker 1976). Indeed, in the last decades an increasing body of studies has laid bare that it is the rule for females from many species to seek or to engage in multiple copulations from multiple partners (Smith 1984; Birkhead and Møller 1998; Simmons 2001; Pizzari and Wedell 2013; Taylor et al. 2014; Garcia-Gonzalez 2017).

Polyandry, when females copulate with multiple males during the same reproductive cycle, implies the temporal and/or spatial overlap of sperm from several males within the female reproductive tract. This fact opens the gates for

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sexual selection to operate after copulation (post-copulatory sexual selection) (Parker 1970a; Eberhard 1996; Tregenza and Wedell 2000; Simmons 2001; Birkhead and Pizzari 2002; Eberhard 2015; Evans and Garcia-Gonzalez 2016; Firman et al. 2017) through mechanisms such as sperm competition (direct male-male competition for the fertilization of a females' ova within the female reproductive tract (Parker 1970a; Simmons 2001)), cryptic female choice (the ability of females to bias the fertilization success of the males that copulate and inseminate them to favour a specific genotype (Eberhard 1985, 1996; Firman et al. 2017)), and postcopulatory sexually antagonistic selection resulting from differences in the evolutionary interests of the two sexes (sexual conflict (Parker 1979; Chapman et al. 2003; Arnqvist and Rowe 2005; Firman 2018)

Polyandry: an evolutionary conundrum

Males and females differ in their investment in reproduction in regard to gamete production and parental care (Parker et al. 1972; Trivers 1972; but see Kokko and Jennions 2008), and consequently each sex follows different strategies to optimize its fitness. In the case of males, the adaptive meaning of multiple mating is easy to understand, the higher the number of mates the higher the probability to sire a greater amount of offspring maximizing in that sense their fitness. Conversely, due to the limitation in the number of ova and the costs derived from reproduction, females use to be choosier regarding mate choice and base their strategy to optimize their fitness in the selection of a good quality mate instead of increasing the number of mating events (Bateman 1948; Andersson 1994). Moreover, mating is a costly process in terms of time and energy consumption, increased risks of predation while mate searching or infection by sexually transmitted diseases (Daly 1978; Magnhagen 1991; Jennions and Petrie 1997, 2000; Lehtonen et al. 2012). Furthermore, females receive, in general, enough sperm in a single copulation to fertilize all their ova. Nonetheless, polyandry is common and taxonomically widespread in nature (Ridley 1990; Jennions and Petrie 2000; Simmons 2001; Zeh and Zeh 2001; Pizzari and Wedell 2013; Taylor et al. 2014).

The questions about the factors underlying the origin and maintenance of polyandrous behaviour have remained an evolutionary conundrum for long time. Two groups of hypotheses have been proposed as potential explanations. On the one hand, some authors have pointed out that polyandry may result as a by-product of a non-adaptive correlated response to selection acting on males. Selection imposes a pressure on males which tend to increase their number of matings to boost their probabilities of siring higher numbers of offspring, maximizing in that sense their reproductive success and consequently their fitness, eveng though such elevated mating rates could be suboptimal for females. Additionally, polyandry has been suggested to result from interlocus sexual conflict. In this case, the so-called 'convenience polyandry' may evolve because the costs derived from male sexual harassment may be even higher than those derived from multiple mating. In that sense, by accepting some additional matings, females can mitigate the costs resulting from the continuous male attempts for mating (Thornhill and Alcock 1983; Halliday and Arnold 1987; Arnqvist and Nilsson 2000

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and references therein; Arnqvist and Rowe 2005; Forstmeier et al. 2011; Garcia-Gonzalez et al. 2015; Harano 2015).

On the other hand, a second group of hypotheses suggests that polyandry could have an adaptive origin rooted on the different benefits that females may obtain by mating with different males. The nature of those benefits is variable, including direct benefits, such as nuptial gifts which provide nutrients and water, access to better territories, fertilization insurance or protection from reproductive harassment among others (Arnqvist and Nilsson 2000; Simmons 2001), but also indirect (genetic) benefits from mating with several males (Yasui 1998; Newcomer et al. 1999; Evans and Magurran 2000; Jennions and Petrie 2000; Garcia-Gonzalez and Simmons 2005; Fisher et al. 2006; Garcia-Gonzalez et al. 2015), including the accruement of good genes or compatible genes that may enhance the viability or the reproductive success of their offspring (Zeh and Zeh 1997; Tregenza and Wedell 1998; Jennions and Petrie 2000; Zeh and Zeh 2001; Garcia-Gonzalez and Simmons 2005; Neff and Pitcher 2005; Simmons 2005; Fisher et al. 2006; Garcia-Gonzalez and Simmons 2007, 2011). Many of the hypotheses based on the benefits of multiple mating are based on the existence of accurate female mate choice. However, assessing the quality of potential mates and making a good choice can be difficult under some circumstances. In some cases, mate choice is unreliable or inexistent, but female multiple mating can be still beneficial. Polyandry has been hypothesized to work as a bet-hedging strategy spreading the risk of mating with unsuitable (e.g., infertile, or genetically incompatible) mates (Philippi and Seger 1989; Yasui 1998; Hopper 1999; Fox and Rauter 2003; Garcia-Gonzalez et al. 2015; Holman 2016; Yasui and Garcia-Gonzalez 2016; Yasui and Yoshimura 2018).

By 'not putting all eggs in one basket' polyandrous females sample more males and may minimize the consequences of assessment errors in mate choice (Yasui 1998; Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016), consequently reducing the risk for females of complete reproductive failure.

In any case, aside which group of hypotheses could be right, it is clear that polyandry has paramount implications, for instance due to its role preventing inbreeding depression and extinction. This may be highly relevant under certain ecological and demographical conditions, for example in small populations in which stochastic changes may have a deep impact and sexual selection cannot operate so effectively (e.g. Tregenza and Wedell 2002; Cornell and Tregenza 2007; Jarzebowska and Radwan 2010; Price et al. 2010; Wade 2010; Holman and Kokko 2013).

Sexual antagonistic coevolution: the tug-of-war for the control of reproduction

It seems to be clear that certain divergence between the interests of males and females is the rule in many species, contrary to the idea of cooperation between sexes accepted in the past (Arnqvist and Rowe 2005, but see Zuk et al. 2014 for taxonomic bias affecting the study of sexual selection and sexual conflict). Sexual selection arising from the competition among males to take reproductive

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advantage over rivals may originate traits that can be beneficial for one sex even though, in some cases, those traits may have a detrimental effect on the opposite sex (e.g. Chapman et al. 1995; Crudgington and Siva-Jothy 2000; Blanckenhorn et al. 2002; Morrow et al. 2003; Wigby and Chapman 2005; Hotzy and Arnqvist 2009; Kimura and Chiba 2015; Reinhardt et al. 2015). Genital traits provide a superb example of this phenomenon (Crudgington and Siva-Jothy 2000; Blanckenhorn et al. 2002; Hotzy and Arnqvist 2009; Dougherty and Simmons 2017; van Haren et al. 2017).

Evidence in support of sexually antagonistic coevolution in male and female genitalia has been found across taxa in the last decades. An increasing number of studies are showing that males and females from multiple species are immerse in a longstanding sexually antagonistic coevolutionary process, similar to an arms race, in which adaptations in one sex for the control over copulation and fitness optimization trigger the evolution of counteradaptations in the opposite sex (e.g. Arnqvist and Rowe 2002b, a; Bergsten and Miller 2007; Brennan et al. 2007; Rönn et al. 2007; Kuntner et al. 2009; Joly and Schiffer 2010; Tatarnic and Cassis 2010; Perry and Rowe 2012; Yassin and Orgogozo 2013; Tanabe and Sota 2014; Brennan and Prum 2015)

The effect of population spatial structure on sexual selection

The opportunity for, and strength of, sexual selection in a population is influenced by many factors including the operational sex ratio (Kokko and Jennions 2008), the availability of sexual partners and the probabilities of mating events (Parker and Simmons 1996), population size, the spatial distribution of the individuals or phenotypic structuring (Gavrilets 2000; Haikola et al. 2001; Gay et al. 2009; Holman and Kokko 2013; McDonald et al. 2013; Fisher et al. 2016; Holman 2016; Yasui and Garcia-Gonzalez 2016; Caballero et al. 2017), and in general ecological, demographic and social factors (see Evans and Garcia-Gonzalez 2016).

Interestingly, recent findings suggest that mating system evolution, and the influence of mating system, and therefore sexual selection, on population persistence over time are closely related to the level of population subdivision (Yasui and Garcia-Gonzalez 2016). The pool of individuals that constitute a population is generally divided in demes that are more or less separated and interconnected, i.e., what is known as metapopulation (Levins 1969; Hanski and Gilpin 1991; Hanski 1998; Hanski 1999). This population spatial structuring is accepted as an important factor mediating critical features of population dynamics as well as population viability and the population's probability of extinction (Hanski 1998; Saccheri et al. 1998; Hanski 1999; Haikola et al. 2001; Nieminen et al. 2001; Hanski and Gaggiotti 2004; Akçakaya et al. 2007; Gilpin 2013). Surprisingly, however, we know very little about the implications of population subdivision for sexual selection and sexual conflict dynamics. When populations are subdivided, the demes may be equivalent to small populations, where the possibilities for selection to operate are limited, leading to inbreeding depression and associated negative effects on the reproductive success of the individuals and population viability (Hartl and Clark 2007), and increasing the probability of

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population extinction simply due to stochastic processes (Martínez-Ruiz and Knell 2017). Moreover, it is important to bear in mind that in small or fragmented populations the number of available mates is limited and a fraction of those would be sterile or genetically incompatible as sexual partners (Zeh and Zeh 1996; Garcia-Gonzalez 2004). Therefore, in small populations or in populations with spatial structure, all these factors may increase the risk of female reproductive failure. In such cases selection may favour polyandrous behaviour because multiple mating, working as a risk-spreading bet-hedging strategy, would minimize the detrimental consequences of mating with unsuitable males (Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016). This in turn, would decrease the probability of extinction of those (small or spatially structured) populations (Yasui and Garcia-Gonzalez 2016).

Yasui and Garcia-Gonzalez's (2016) study investigated these issues from a theoretical point of view, using computer simulations. However, empirical studies into the connections between population spatial structure and sexual selection (or sexual conflict, for that matter) are lacking. Addressing this gap in knowledge is precisely the main objective of this thesis.

Using the right tools to get new insights

In order to shed light into the role of metapopulation structure upon the dynamics of sexual selection and sexual conflict a suitable model system and proper experimental techniques are required. The experiments of the present doctoral thesis have been carried out using *Callosobruchus maculatus*, (Fabricius), a seed beetle from the family Bruchidae (Kingsolver 2004; Ramos et al. 2007). *C. maculatus* is a popular model system for the study of sexual selection and sexual conflict (Crudgington 2001; Arnqvist et al. 2004) due to, among other reasons, conspicuous sexual dimorphism in structures and behaviours, short generation times, and the fact that it is easy to rear under laboratory conditions (see Chapter 1 for details). *C. maculatus* exhibits genital traits and copulatory behaviours that are believed to be shaped by sexually antagonistic coevolution (Rönn et al. 2007). For example, males possess genital spines covering the tip of the aedeagus (intromittent organ), which provide benefits for males regarding their reproductive success but damage the female reproductive tract during copulation (Crudgington and Siva-Jothy 2000; Edvardsson and Tregenza 2005; Eady et al. 2007; Hotzy and Arnqvist 2009). Females on the other hand have a thick layer of connective tissue in the walls of the female bursa copulatrix, thought to have evolved to ameliorate the genital damage inflicted by males (Rönn et al. 2007; but see Cayetano et al. 2011) . Females also exhibit a pericopulatory female behavior, so-called kicking, in which females kick the mounting males using their hind legs during the last third of the mating events (Crudgington and Siva-Jothy 2000; Edvardsson and Tregenza 2005; Edvardsson and Canal 2006; van Lieshout et al. 2014; Wilson and Tomkins 2014).

The use of this model system has been combined with experimental evolution, a methodological approach considered nowadays one of the most powerful tools in the study of evolution (Garland and Rose 2009; Garcia-Gonzalez 2011; Kawecki et

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al. 2012). In experimental evolution the researchers replicate evolution under controlled conditions. To that purpose, a certain selective pressure is imposed on individuals and then the researchers investigate the changes in traits across generations by comparing experimental and control populations, offering exceptional real-time insights into adaptation and evolutionary processes. Over the last decades, experimental evolution has been used by an increasing body of studies to unveil the forces driving the evolution of the organisms and populations. A good example of its relevance is the crucial role it has played in the studies which have tried to shed light on the links between sexual selection and the phenotypic evolution of the organisms, the population viability or the evolution of the sexual conflict dynamics for example (e.g. Holland and Rice 1999; Pitnick et al. 2001a; Pitnick et al. 2001b; Martin and Hosken 2003; Friberg 2005; Rice and Holland 2005; Kelly et al. 2006; Crudgington et al. 2010; Gay et al. 2010; Cayetano et al. 2011; Hollis and Houle 2011; Arbuthnott and Rundle 2012; Almbro and Simmons 2014; Simmons and Firman 2014; Lumley et al. 2015).

A brief outline of this doctoral thesis

The present doctoral thesis has been divided in six chapters through which we have pretended to shed light into some of the aforementioned evolutionary questions.

To achieve that purpose, our first step was the creation of four different selection regimes resulting from the combination of a mating system selection treatment (two levels: monogamy vs. polygamy) and a population spatial structure selection treatment (two levels: presence or absence of population subdivision) following a 2x2 full factorial design.

In the first chapter, we introduce the general framework describing in detail both the model system and the experimental design we followed to set up the selection regimes and the near-isogenic lines to generate the focal and tester individuals used in each of the experiments explained in the subsequent chapters.

In the second chapter we explore the effects of selection arising from variation in mating system and population spatial structure, separately and in combination, on the individuals body size. This is an important trait from an evolutionary perspective because of its tight association with reproductive success and survival, and consequently, with fitness (LaBarbera 1989; Blanckenhorn 2000; Nijhout 2003; Parker and Johnston 2006; Chown and Gaston 2010). Additionally, we delved into the role of our selection treatments on the evolution of sexual size dimorphism in this chapter.

In Chapter 3, we gather data and analyze the mating rates of females from the different selection regimes to determine the role of spatial population structure on mating frequency rates, providing with this enquiry the first empirical test for the predictions generated by Yasui and Garcia-Gonzalez (2016).

Sexual selection is thought to play a crucial role determining the viability of a population by leading to faster adaptation, facilitating the removal of deleterious

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alleles and/or reducing inbreeding depression, and ultimately reducing the probability of population extinction (Tregenza and Wedell 2002; Whitlock and Agrawal 2009; Jarzebowska and Radwan 2010; Holman and Kokko 2013). However, population viability and its probability of extinction may also be mediated by population spatial subdivision (Hanski 1998; Saccheri et al. 1998; Hanski 1999; Haikola et al. 2001; Nieminen et al. 2001; Hanski and Gaggiotti 2004; Akçakaya et al. 2007; Gilpin 2013). In Chapter 4, we test empirically for the first time the independent and combined effects of mating system and population spatial structure selection history on population productivity and female survival, two traits closely linked to the viability and probability of extinction of populations.

In chapter 5, we explore the role of population spatial structure and its interactive effect with the presence or absence of sexual selection upon the evolution of sexual conflict adaptations in males and counter-adaptations in females.

Finally, in the sixth and last chapter, we explore the effect of the presence or absence of sexual selection in combination with the population spatial structure on the coevolution between male and female genital traits. To this purpose, we analyze the evolution of the male genital spines and the amount of connective tissue in the walls of the bursa copulatrix of females coming from our different selection regimes.

All the chapters in this thesis, apart from Chapter 2, are manuscripts that will be submitted soon for their publication in international scientific journals. For this reason, the format and structure of those chapters conform to that of manuscripts, and include details about authors, affiliations and funding.

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Objectives

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Objectives

The present PhD thesis is principally aimed at studying the evolution of sexual selection and sexual conflict dynamics in response to selection imposed by variation in population spatial structure and variation in mating system.

This main objective has been addressed through the different chapters of this thesis. The specific objectives of the thesis are:

1) To evaluate the effects of the selective pressures imposed by the selection treatments regarding mating system and population spatial structure, separately and in combination, on the evolution of body size and sexual size dimorphism (Chapter 2).
2) To empirically assess the potential role of population subdivision driving variation in female mating frequency (Chapter 3).
3) To evaluate the influence of mating system and associated direct and indirect benefits related to multiple mating, together with population subdivision, on the viability of the populations and their probability of extinction (Chapter 4).
4) To investigate the evolution of sexual conflict traits, and in particular the evolution of male harm (to females) and female resistance (to male harm), in response to the manipulation of mating system and population spatial structure selection history (Chapter 5).
5) To determine whether selection arising from variation in mating system and population spatial structure fuels sexually antagonistic coevolution between male and female genital traits (Chapter 6).

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Chapter 1

General material and methods. Model system and the experimental evolution approach

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Abstract

A suitable model system and proper methodologies are important elements in research. In this chapter I describe, in the first place, a series of ecological and physiological features that make the seed beetle *Callosobruchus maculatus* a suitable study model to address evolutionary questions in regards to the evolution of sexual selection and sexual conflict dynamics. Secondly, I describe how we have used experimental evolution establishing four different selection regimes combining mating system (monogamy / polygamy) and spatial population structure (structure / no structure), to unveil the main and interactive effects of these two selection treatments on individual and population traits. I also provide the details concerning the generation of a series of near-isogenic lines exhibiting a standard, homogeneous genetic background, which we have used to generate tester individuals in the experiments in this thesis. Finally, I outline the common garden design followed in certain generations to separate genetically assimilated differences among the selection regimes from parental and environmental effects attributable to breeding conditions.

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STUDY ANIMALS

The study model used to carry out the experiments of this thesis was *Callosobruchus maculatus* (Fabricius), a seed beetle from the family Bruchidae also known as cowpea weevil or bean beetle (Kingsolver 2004; Ramos et al. 2007). This species is a pest of stored products that is distributed all over the planet (Southgate 1979; Utida 1981; Fox 1993). This status is favoured by several ecological characteristics of the species such as: a short generation time (25-40 days depending on temperature and humidity conditions), high mating rates and a polygamous strategy in natural populations, the fact that individuals from both sexes can reproduce soon after adult emergence (Utida 1972; Fox et al. 2003), and the fact that females are able to lay eggs quickly after mating favouring the colonization of new patches of resources. Furthermore, this seed beetle may infest several species of beans and other legumes, which are used as oviposition substrates and which provide the resources needed for larval development and completion of the life cycle (Paukku and Kotiaho 2005). In addition, emerging adults do not need food or water to be able to reproduce, as they can survive on resources accrued during larval stages (Savalli and Fox 1999b). All these attributes, and in particular, the short generation time and ease of laboratory rearing make this species a suitable model for experimental evolution studies (see below).

C. maculatus may exhibit two distinct, density-dependent adult forms, called "flightless" (normal) and "flight" forms, which differ not only in terms of morphology but also in their biology and behavior (Utida 1972; 1981 and references therein). Beetles from the flightless form typically copulate soon after emerging and females generally lay a total of 60-70 eggs during adult life (Utida 1956). On the contrary, beetles from the flight morph have a greater tendency towards flying and dispersal and copulate a little bit later in their life. Larval crowding, temperature and the water content of the oviposition substrate are among the factors that trigger the emergence of the "flight" morph. For all the work in this thesis we have ensured low levels of larval competition, which has resulted in negligible levels of emergence of the "flight" form (Utida 1972 and references therein).

Males and females of the 'flightless form' are easy to differentiate according to several traits. In general females tend to be larger in size than males (Savalli and Fox 1999a). In addition, females present a blackish coloration with two big specks in the middle region of the elytra, while males present a uniform brownish coloration without the big pair of central specks or smaller in size when these are present. However, the most distinctive trait easing the differentiation of sexes is the shape and coloration of the posterior abdominal plate (pygidium). This region is elongated and darkly colored on both sides in females, but smaller and paler, and with a lack of stripes, in males (Halstead 1963; Beck and Blumer 2011) (See Fig. 1.1).

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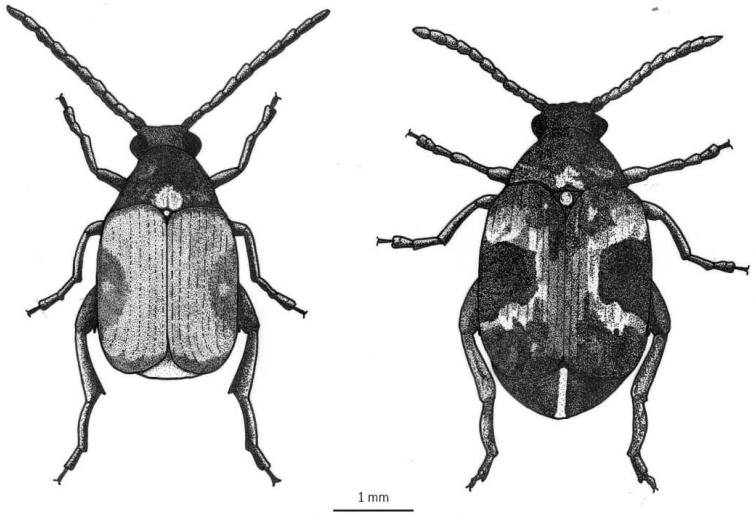

Fig. 1.1 Male (left) and female (right) of the 'flightless' form of *C. maculatus*. In general, both sexes can be distinguished paying attention to the size and the coloration of the elytra and the pygidium. Drawn by Eduardo Rodriguez-Exposito.

Life cycle

Our beetles were cultured on mung beans (*Vigna radiata*; hereafter I will refer to this oviposition substrate simply as beans). A large fraction of the life cycle of this species occurs inside the seeds that they infest. After mating the inseminated female glues a single egg on the surface of the bean. Around five days later the first larval instar hatches and burrows into the bean's endosperm where it remains for 15 – 18 days as larvae, then pupa and finally an adult, which emerges from the bean chewing through the bean coat (Southgate 1979; Beck and Blumer 2011). Under our laboratory conditions, the whole life cycle, from newly laid eggs to the emergence of adults, lasted 21-24 days (Fig. 1.2).

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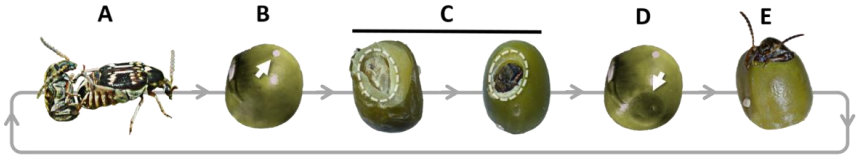

Fig. 1.2. Lyfe cycle of *C. maculatus*. After mating (A), female glues an egg on the surface of the bean (B). A few days later, the first larval instar burrows into the seed where it remains feeding and going through the different developmental phases (C). Once the individual has reached the last developmental stage, it is possible to notice a dark window on the surface of the bean (D). A fully developed adult emerges from the bean chewing through the bean coat where the window was formerly located (E). Images taken by Eduardo Rodriguez-Exposito.

Mating behaviour

This species exhibits an interesting mating behavior that has been meticulously described (Rup 1986). The different aspects of the mating behaviour of *C. maculatus* have been analyzed in detail in several studies before, partly because this beetle is a model organism for studies of sexual conflict (e.g. Crudgington 2001; Arnqvist and Rowe 2005; Rönn et al. 2007; Zuk et al. 2014), as it will be exposed in Chapter V. Briefly, upon encountering a female the male approaches her and waves his antennae. Then, the male taps her body with his antennae while rising his own body from the substrate. At this phase, the male mounts the female from the rear and starts to palpate and tap with his antennae the sides of the female body. Holding the female in such position, the male protrudes his aedeagus and starts to make probing strikes until he succeeds in the intromission of the aedeagus into the female reproductive tract (Rup 1986). At that moment, the male progressively decreases the movement of his antennae and starts to move his body slowly back and forward while transferring his ejaculate to the female. The end of this phase is determined by the female which starts to kick the male with her hind legs to dislodge him. The start of female kicking takes place approximately once the copulation has reached over two thirds of its overall duration (Edvardsson and Tregenza 2005 and references therein, but see ; Wilson and Tomkins 2014).

In this species, the male's intromittent organ (aedeagus) is densely covered by spines that inflict injuries to the female reproductive tract during copulation (Fig.1.3), and that ultimately reduce female lifespan (Crudgington and Siva-Jothy 2000; Edvardsson and Canal 2006; Eady et al. 2007). Sexual conflict and sexually antagonistic coevolution (Rice 1996; Holland and Rice 1999 and see Chapters V and VI) have favoured the development of several traits in females that ameliorate the damage produced by males. For example, from a comparative perspective it has been demonstrated that across several species of bruchids, those species in which males present larger spines in the aedeagus, the bursa copulatrix of the females contains a higher amount of protective connective tissue (Rönn et al. 2007). Evidence for sexual coevolution has also been recently provided at the within-

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species level (Dougherty et al. 2017). Furthermore, as explained briefly above, females of *C. maculatus* exhibit a 'kicking' behaviour in which the females kick the males using their hind legs during the last third of the mating event (Eady 1991). Initially, this behavior was described as a female attempt to shorten copulation duration to avoid the damage derived from mating by dislodging the male once the female has received enough ejaculate to ensure egg fertilization (Edvardsson and Tregenza 2005; Edvardsson and Canal 2006). However, the function of this behavior remains controversial (e.g. Wilson and Tomkins 2014; Dougherty and Simmons 2017; Dougherty et al. 2017 and see Chapter V). What seems clear, nonetheless, is that both sexes are immersed in a coevolutionary 'arms race' to gain control over several aspects of the mating interaction (see Chapters V and VI).

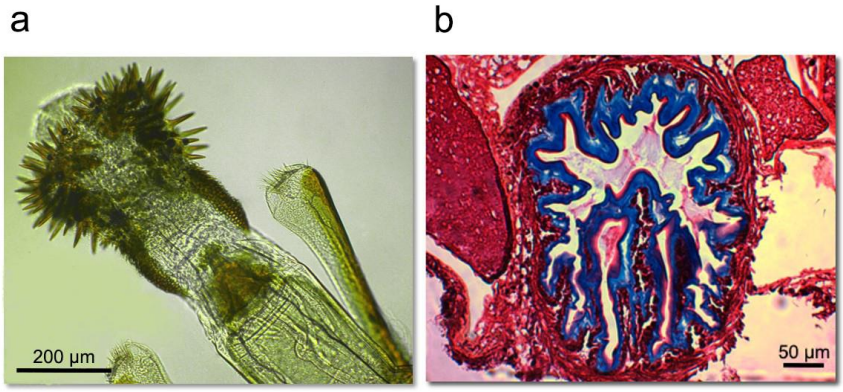

Fig. 1.3. Details of male and female genitalia. Males possess a spiny aedeagus which inflicts damages to the female (a) by puncturing the female reproductive tract during copulation (see Chapters V and VI). As a result of antagonistic coevolution, females are selected to increase the amount of connective tissue (in blue) in the walls of the bursa copulatrix (see Chapter VI) so that the harm inflicted by the spines is ameliorated (b). Images taken by Eduardo Rodriguez-Exposito.

STOCK POPULATION

The populations used in our experiments were sourced from an outbred population (South Indian stock population -SI USA-) that presents substantial phenotypic and genetic variance for a range of traits and behaviours (see results within this thesis, Zajitschek et al. unpublished, and Fox et al. 2003; Fox et al. 2004; Bilde et al. 2008; Berg and Maklakov 2012; Berger et al. 2014). This population was obtained from a replicate held at Uppsala University and prior to this kept by C. W. Fox at the University of Kentucky. The SI USA population was originated from infested mung beans (*Vigna radiata*) collected from Tirunelveli, India, in 1979 (Mitchell 1991; Fox et al. 2004). We established our stock populations in 2013 with a large number of

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beetles (>450 founders from two batches that were mixed) from the replicate SI population held at Uppsala University, and have cultured it since then on organic mung beans (*Vigna radiata*) that are frozen prior to use.

The population in our lab is typically maintained across 3-4 replicated population containers. Each generation and from each container, two days after the emergence of the firsts adults, 50 non-virgin individuals (25 males and 25 females) are randomly selected and transferred to a new container with clean beans ad libitum, to generate the next generation of beetles. Matings and oviposition are allowed for 48 hours, after which the 50 reproducing adults are removed from the containers. The effective population size for each replicated population exceeds 75 individuals, due to the use of non-virgin females and the high rates of female multiple mating in these populations. Usually around a thousand adult beetles emerge from each of these containers, and individuals from the different replicated populations are mixed every few generations. Thus, we keep the stock population with large population sizes (in excess of 300 individuals) and non-overlapping generations. Beetles from the stock population, selection lines and inbred lines (see below) are all kept in climate chambers Fitoclima 10.000 EHF (Aralab, Portugal) at 29 °C, 40% relative humidity, and a 12L: 12D cycle. Under these conditions egg to adult development occurs in 21-24 days.

THE EXPERIMENTAL EVOLUTION APPROACH: Manipulating selection arising from variation in population spatial structure and mating system

1. Selection lines

We used experimental evolution to gain insights into the effects of variation in population spatial structure and mating system on the dynamics of sexual selection and sexual conflict. Using the SI USA stock population, we set up a selection protocol consisting in the combination of two selection treatments: population spatial structure (presence or absence) and mating system (monogamy or polygamy; i.e., absence and presence of sexual selection and sexual conflict, respectively; see below). Briefly, 8 populations (henceforth metapopulation lines) derived from the stock population were each subdivided into 5 subpopulations, while another 8 populations derived from the same source population were kept as controls (i.e., undivided). Individuals from the source population were randomized among these groups, keeping an equal sex ratio, and all the populations were originated and maintained with 50 breeders each (25 females and 25 males). Importantly, half of the lines in each level of the population structure treatment have been kept under monogamy and the other half under polygamy. Polygamy works as the control group in the mating system selection treatment because *C. maculatus* is naturally polygamous.

In the polygamous lines (n = 8), sexual interactions and matings occur in an unrestricted way among all the individuals in the population (for the lines without population structure) or subpopulation (for the metapopulation lines). In the monogamous lines (n = 8), sexual interactions occur on a one male-one female basis. The mating system treatment effectively enforces the removal of sexual selection

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and ensuing sexual conflict in the monogamous lines because in these lines there is no room for precopulatory or postcopulatory female choice or male-male competition (Holland and Rice 1999; Simmons and Garcia-Gonzalez 2008).

In short, the selection experiment consisted of a 2 x 2 design (sexual selection treatment x spatial population structure treatment), with 16 lines (see Fig.1.4A):
- 4 lines under polygamy (sexual selection present) and absence of population structure: non-structure and polygamy (henceforth **NSPoly**) lines.
- 4 lines kept under polygamy and spatial population structure: structure and polygamy (henceforth **SPoly**) lines.
- 4 lines of beetles with a selection history of monogamy (sexual selection and sexual conflict absent) and absence of population structure: non-structure and monogamy (henceforth **NSMono**) lines.
- 4 lines of beetles under monogamy and spatial population structure: structure and monogamy (henceforth **SMono** lines).

The work in this thesis focuses on experiments and work done up to generation 47 of the selection protocol.

A critical aspect of metapopulation structure is the presence of some degree of gene flow among demes (Hanski 1998; Hanski 1999; Hanski and Gaggiotti 2004). We implemented a moderate migration rate within the experimental evolution approach for the lines with spatial structure. In each generation 20% randomly chosen individuals from each subpopulation (i.e., one male and one female per subpopulation) were forced to migrate (i.e., were relocated) to a different subpopulation within each metapopulation line (Figure 1.4B). This relocation was carried upon adult emergence using virgin individuals (see details below for the protocol ensuring adult virginity). The imposed migration thus effectively introduces gene flow among subpopulations, as it happens in natural metapopulations, but it does not alter other aspects of the selection protocol (for instance, the levels of sexual interactions imposed) otherwise. A summary of the scope for sexual interactions and the offspring pooling protocol within each selection treatment is provided in Figure 1.4C.

Sexual interactions and ensuing egg laying by females were allowed across all lines for two days (Day 1 and Day 2 of the experimental cycle). The number of beans per female was standardized (see below) to ensure *ad libitum* oviposition substrate so as to make sure that larval competition was mostly absent (Colegrave 1993; Horng 1997). On Day 3 adults were removed from the containers (see details below) hosting the animals. On Day 10 we randomly selected 150 inoculated beans from each line. The great majority of the inoculated beans across all treatments had only one egg per bean, indicative of a lack of competition among females for beans. Each of the randomly selected inoculated beans (n = 2400 per generation across the 16 lines) was isolated into an eppendorf tube with pinholes in the cap to allow airflow (henceforth "isolation chamber") and kept until adult emergence (starting typically on Day 21). This protocol ensured virginity of the individuals to be used as breeders for the next generation. Virgin adults were collected randomly among those emerged between Day 21 and Day 24 of the cycle so as to avoid inadvertent selection on early maturation (i.e., development time) (Maklakov et al. 2010). Typically nearly all individuals emerged within these days. After Day 25 the cycle started again,

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setting up 1-4 day-old individuals as breeders for the next generation (Day 1 of the experimental cycle).

The selection of inoculated beans from each line to generate the next generation of animals was carried out randomly but to avoid unintended selection we followed a systematized plan for the propagation of the lines. This plan also ensured that we imposed the appropriate levels of sexual interactions envisaged by the experimental design:

- Non-structure and polygamy (NSPoly) lines: The 25 breeding couples per line were placed in a 750 ml plastic container with approx. 1600 beans (64 seeds per female). As mentioned above, as for the rest of the selection lines, sexual interactions and egg laying took place during two days. For each line, the 50 breeders for the next generation were randomly selected from the virgin adults emerging from the 150 inoculated beans haphazardly collected from the population container (beans subsequently kept in isolation chambers as described above, for all lines in the selection experiment).
- Structure and polygamy (SPoly) lines: For each of the 5 subpopulations within each line we placed five breeding couples in a 140 ml plastic container with approx. 320 beans (64 seeds per female). Thirty inoculated beans per subpopulation (i.e., 150 per line) were randomly selected to source the breeders for the next generation. A random selection of 4 virgin males and 4 virgin females emerged from the beans in each subpopulation plus another couple of virgin adults emerging from the beans in a different subpopulation (imposed migration, see above and Fig. 1.4B) were designated as the subpopulation breeders for the next generation. Thus, within each line metapopulation structure was mimicked (with gene flow among subpopulations allowed by a 20% migration rate) and individuals could engage in polygamous sexual interactions.
- Non-structure and monogamy (NSMono) lines: The 25 breeding couples per line were each placed in a 30 ml plastic container with 64 beans (i.e., 64 beans per female). Six inoculated beans per container, that is, from each female (i.e., 150 beans per line), were randomly selected. The breeders for the next generation were then randomly sourced from the virgin adults emerging from the pool of 150 beans collected in each line. Thus, within each of these lines, monogamous matings were enforced and there was no population subdivision whatsoever (breeders originated from the pool of 150 beans).
- Structure and monogamy (SMono lines). In this treatment, as in SPoly lines, there were 5 breeding couples for each of the 5 subpopulations in each line. However, monogamy was enforced because each male-female pair was housed in a 30 ml plastic container (with 64 beans). Six inoculated beans per container were randomly collected, as in the NSMono lines; however, to impose the effects of spatial population structure, inoculated beans were not pooled at the population level (as in NSMono lines) but at the subpopulation level (n = 30 inoculated beans per subpopulation, n beans per line = 150). Like SPoly lines, a random selection of 4 virgin males and 4 virgin females emerged from the beans in each subpopulation plus another couple of virgin adults emerging from the beans in a different subpopulation (imposed migration, see above and Fig. 1.4B) were designated as the subpopulation breeders for the next generation. Therefore, within each of these lines, metapopulation structure was mimicked (with limited gene flow among subpopulations) and sexual selection was removed (individuals could only engage

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in imposed monogamous sexual interactions).

As it can be seen from the description above, the ratio of number of females to number of beans was low and constant across all treatments to ensure that larval competition was not an issue and that no differences among treatments could arise in regards to this factor. We also ensured, as previous studies (Maklakov et al. 2010), that we did not impose selection for early maturation because we collected adults randomly among those emerged along the four days following the beginning of the emersion phase (Days 21 to 24 in the experimental cycle).

2. Common garden breeding.

Several assays on the evolutionary divergence of traits from the individuals from the selection lines were carried out after 1 or 2 generations of common garden in the form of polygamous breeding under absence of spatial population structure. In this way any divergence in the traits assayed could be attributed to genetic effects (i.e., evolutionary effects genetically assimilated) rather than to maternal/paternal or other environmental effects arising from the type of breeding (Simmons and Garcia-Gonzalez 2008; Garland and Rose 2009; Garcia-Gonzalez 2011; Kawecki et al. 2012). To this end, we replicated the selection protocol starting with the duplication of the number of inoculated beans collected from each line. We then kept the selection protocol on as always, and used the additional beetles to establish a set of 16 replicated common garden lines all under NSPoly conditions.

3. Tester individuals from near-isogenic lines

Traits that needed to be measured following the interaction between the two sexes were assayed on focal animals from the selection lines using tester individuals that were sourced from outside the selection experiment. In this way confounding effects due to (within-line) male-by-female coevolution were controlled for (e.g. Holland and Rice 1999). Further, to standardize the background upon which traits in experimentally evolved beetles were measured, tester individuals were obtained from near-isogenic lines of *C. maculatus*. Each of these lines was started with one founder male-female pair from the stock population and the line was propagated through a full brother- full sister mating protocol that spanned many generations (>15, see specific Chapters for details about the number of generations in each case). Some assays were carried out using tester individuals from such pure near-isogenic lines. In other cases, tester individuals were obtained after crossing two near-isogenic lines. These crosses were carried out to generate a standardized (but heterozygous) genetic background (Garcia-Gonzalez and Dowling 2015). We call the lines from these crosses Standardized Heterozygous Lines (SHL). These lines were generated to avoid undesired effects of inbreeding potentially present in near-isogenic lines (Tran and Credland 1995; Fox et al. 2007; Harano 2011), which could obscure the interpretation of results. Crosses leading to SHL lines were established by housing together in a 750 ml plastic container 25 males and 25 females collected from two randomly chosen near-isogenic lines (12 and 13 beetles from each sex from each near-isogenic line) two generations before carrying out the assays. These lines were kept with a non-overlapping generations protocol in which within-line

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matings (25 males and 25 females) were allowed. Likewise, when pure near-isogenic lines were used, two generations before the assays 25 pairs from each line were transferred to 750 ml containers and within-line matings allowed under a non-overlapping generations protocol. This punctual "mass-breeding" within-line protocol ensured the production of enough tester animals for the assays.

Traits measured in focal animals for any given assay were tested with individuals sourced from the same pure near-isogenic line or SHL; we thus standardized the genetic background to measure experimentally evolved individuals. This degree of experimental control is especially important when assaying traits that are influenced by interacting phenotypes because it minimizes sampling variance arising from the random sampling of mates that differ in their effects on the traits measured in the focal individuals (see for rationale and application Garcia-Gonzalez and Evans 2011; Garcia-Gonzalez and Dowling 2015; Travers et al. 2015; Travers et al. 2016).

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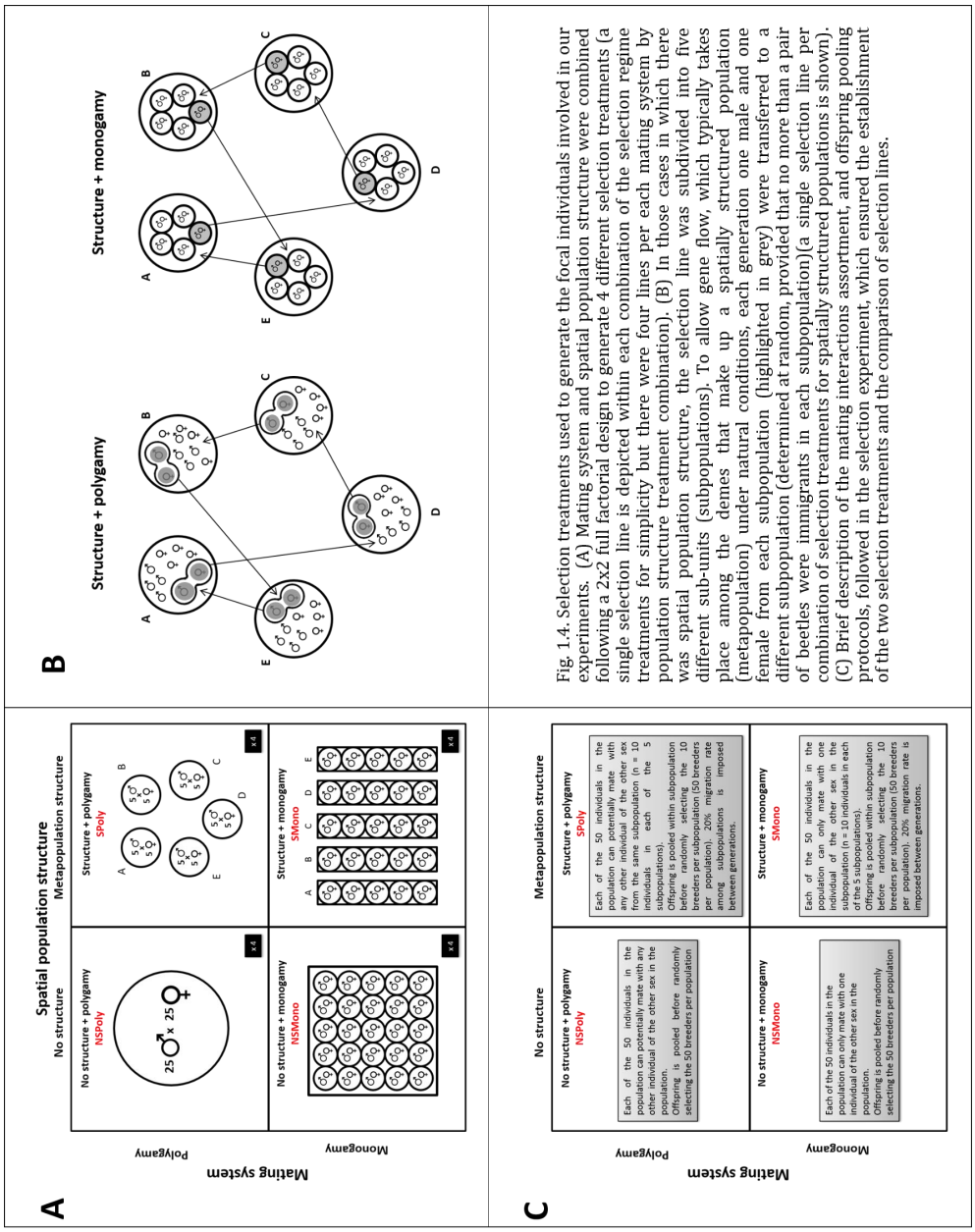

Fig. 1.4. Selection treatments used to generate the focal individuals involved in our experiments. (A) Mating system and spatial population structure were combined following a 2x2 full factorial design to generate 4 different selection treatments (a single selection line is depicted within each combination of the selection regime treatments for simplicity but there were four lines per each mating system by population structure treatment combination). (B) In those cases in which there was spatial population structure, the selection line was subdivided into five different sub-units (subpopulations). To allow gene flow, which typically takes place among the demes that make up a spatially structured population (metapopulation) under natural conditions, each generation one male and one female from each subpopulation (highlighted in grey) were transferred to a different subpopulation (determined at random, provided that no more than a pair of beetles were immigrants in each subpopulation)(a single selection line per combination of selection treatments for spatially structured populations is shown). (C) Brief description of the mating interactions assortment, and offspring pooling protocols, followed in the selection experiment, which ensured the establishment of the two selection treatments and the comparison of selection lines.

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Chapter 2

Sex-specific patterns of body size evolution revealed by experimental evolution of mating system and population spatial structure

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Sex-specific patterns of body size evolution revealed by experimental evolution of mating system and population spatial structure.

Eduardo Rodriguez-Exposito [1] and Francisco Garcia-Gonzalez [1,2]

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Abstract

Body size is one of the most important traits of an organism due to its general tight association with body condition, survival and reproductive success. It is widely accepted that body size evolution is influenced by viability, fecundity and sexual selection, but the action of selection may differ between sexes leading to sexual size dimorphism (SSD). Little is known in relation to the effects of presumably important ecological and demographic factors such as population spatial structure on the evolution of body size and SSD. Here, we used the bean beetle *Callosobruchus maculatus*, which exhibits SSD, in an experimental evolution approach to evaluate the main and interactive effects of sexual selection and selection arising from variation in the population spatial structure on the evolution of body size and the magnitude of SSD. Our results indicate sex-specific patterns of body size evolution. The magnitude of SSD varied in relation to sexual selection, increasing in those populations evolving under enforced monogamy, where sexual selection was experimentally removed. Additionally, an effect of the mating system on the individual's body mass was detected but this effect disappeared after one generation of common garden suggesting that the differences we observed were mainly driven by parental and/or other environmental effects rather than by selection arising from selection history. Selection arising from variation in population spatial structure seemed not to have an effect on the evolution of body size and SDD.

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Introduction

From an evolutionary perspective and due to its tight association with components of fitness, body size is arguably amongst the most important traits of an organism (LaBarbera 1989; Blanckenhorn 2000; Nijhout 2003; Parker and Johnston 2006; Chown and Gaston 2010). The role of natural and sexual selection shaping body size is evident, for instance, by the well-known associations between this trait and resource acquisition, mating success, or survival (e.g. Roff 2002; Blanckenhorn et al. 2007; Briffa and Sneddon 2007; Serrano-Meneses et al. 2007; Teuschl et al. 2007; Moore et al. 2009; Han and Jablonski 2010). Furthermore, an individuals' body size may impact demographic aspects indirectly, due to the implications it has regarding survival and reproductive success (Eady 1991; Savalli and Fox 1999; Blanckenhorn 2000; Schulte-Hostedde 2007; Chown and Gaston 2010).

Viability selection, fecundity selection and sexual selection are the three major forces underlying body size evolution. Fecundity selection typically favours larger body size in females, while sexual selection usually influences males to a larger extent (Andersson 1994; Blanckenhorn 2000; Fairbairn et al. 2007). For females, larger body size increases lifetime fecundity, offspring survival (through, for example, higher-quality maternal care) and female lifespan, for instance if larger body size facilitates access to resources (Fox 1993; Savalli and Fox 1999; Blanckenhorn 2000). For males, larger body size generally enhances male reproductive success by means of increasing a male's access to mates (pre-copulatory sexual selection either through female mate choice or male-male competition, or by both mechanisms) and/or access to the ova in sperm competitive contexts (post-copulatory sexual selection: sperm competition and/or cryptic female choice, CFC) (e.g. Eady 1991; Andersson 1994; Fox et al. 1995; Savalli and Fox 1999; Bangham et al. 2002; Bertin and Cezilly 2003; Maklakov et al. 2004; Clutton-Brock 2007; Fairbairn et al. 2007; Evans and Garcia-Gonzalez 2016).

Being large implies therefore a series of advantages generally. However, it may come with downsides (Blanckenhorn 2000; Roff 2002). A large body size is typically associated to larger energy costs. Becoming large implies that the individuals need to invest more time in development, grow faster or augment nutrient intake to maintain a larger size. This may often result in higher risks of predation, parasitism and starvation. There are thus many reasons for which selection imposes a limit to body size, or favours smaller sizes. Small individuals are more agile (Moya-Laraño et al. 2002; Crompton et al. 2003), less prone to be detected by predators (Wellborn 1994), and they need less resources to self-maintenance (Blanckenhorn et al. 2007). Small individuals can invest time and energy that is not diverted to self-maintenance to different activities (e.g., courting, searching for mates, foraging, etc.), which can increase their reproductive success through alternative ways compared to larger individuals (Andersson 1994; Blanckenhorn 2005 and references therein). Therefore, the body size of an individual depends on the balance between the benefits and costs that a certain body size entails and the underlying trade-offs among size-related traits (Blanckenhorn 2000; Roff 2002; Serrano-Meneses et al. 2007; Kasumovic and Andrade 2009).

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Interestingly, selection can lead to differences in body size between the two sexes, that is, to sexual size dimorphism (hereafter SSD). The magnitude of SSD is determined by the equilibrium among the selection pressures acting on size in males and females (Shine 1989; Delph 2005; Fairbairn et al. 2007). The body size that maximizes fitness frequently differs for each sex (e.g. Fairbairn 1997; Blanckenhorn 2000; Fairbairn et al. 2007 and references therein). This fact fuels an evolutionary genomic conflict because identical set of genes must lead to divergent optimal phenotypes for each sex (Preziosi and Fairbairn 2000; Gibson et al. 2002; Bonduriansky and Rowe 2005; Fairbairn et al. 2007; Bonduriansky and Chenoweth 2009). Indeed, the differences in the evolutionary interests of males and females (sexual conflict (Parker 1979; Arnqvist and Rowe 2005)) may play an important role in the evolution of body size and SSD in some species, such as for instance *Drosophila melanogaster* (e.g. Pitnick et al. 2001; Pitnick and Garcia–Gonzalez 2002; Friberg and Arnqvist 2003).

Male-biased SSD is normally attributed to sexual selection favouring larger males which have higher probabilities to win in male-male competition events. On the other hand, asymmetric selection favouring more fecund females (the fecundity-advantage hypothesis), or small mobile males (the small-male advantage hypothesis) has been invoked as one of the reasons underlying female-biased SSD (Zamudio 1998).

Experimental evolution is a powerful tool to study evolution (Garland and Rose 2009; Garcia-Gonzalez 2011; Kawecki et al. 2012), including the evolution of body size (e.g. Kelly et al. 2006; Stillwell et al. 2008; Amarillo-Suárez et al. 2011). In particular, experimental evolution approaches investigating adaptation in response to sexual selection have recently provided important insights into body size evolution (e.g. Hosken et al. 2001; Friberg 2005; Cayetano et al. 2011; Snook et al. 2013; Simmons and Firman 2014). A common protocol in most experimental evolution studies to investigate this question compares selection lines evolving under a polygamous mating system (i.e., where sexual selection is present) against selection lines in which sexual selection is removed (e.g., by enforcing monogamy) (e.g. Pitnick et al. 2001; Simmons and Garcia-Gonzalez 2008; Simmons et al. 2009; Cayetano et al. 2011). In some species, such as in *D. melanogaster*, the removal of sexual selection leads to the evolution of smaller male body size and testes size, with a concomitant reduction in the sperm numbers, linked in turn to a clear disadvantage regarding male reproductive competitiveness (Pitnick et al. 2001). In other study models, the release from sexual selection has been proved to have an effect on the size of genital traits or other morphological traits, but not on body size (Simmons and Garcia-Gonzalez 2008; Yamane et al. 2010; Cayetano et al. 2011; Simmons and Garcia-Gonzalez 2011). These examples illustrate that there is mixed evidence regarding the impact of sexual selection on body size evolution, which in turn reflects that our understanding of the evolutionary causes and consequences of variation in body size is incomplete. Furthermore, we know very little of whether, and how, other presumably important ecological and demographic factors moderate body size evolution and SSD. One such factor is population spatial structure (metapopulation structure).

A metapopulation is an ensemble of populations connected by dispersing individuals (Hanski and Gilpin 1991; Haikola et al. 2001). Metapopulation

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structure limits to some extent the interaction among individuals at both inter- and intra-specific levels, e.g. predation dynamics due to prey availability (Hanski and Gaggiotti 2004), or mating opportunities due to a limitation of potential mates (Yasui and Garcia-Gonzalez 2016; Muniz et al. 2017; Yasui and Yoshimura 2018). Metapopulation structure has important ramifications upon many population -and individual- based traits (Hanski 1998). Population spatial structure is generally associated to variation in genetic diversity, inbreeding and mutation loads, which in turn are important factors underlying the viability and fitness of the individuals and populations (Saccheri et al. 1998; Haikola et al. 2001; Hartl and Clark 2007). Surprisingly, despite the multiple effects that metapopulation structure may impose at different levels, the influence of population spatial division on the strength and opportunity of sexual selection is largely unknown (see below). Likewise, the effects of metapopulation structure on body size evolution are largely unexplored.

Recent research has revealed that variation in the degree of population spatial structure may have far reaching implications for mating system evolution (Yasui and Garcia-Gonzalez 2016). Specifically, population subdivision has been found to favour the evolution of polyandry (when females mate with multiple males within a same reproductive episode; see (Yasui and Garcia-Gonzalez 2016)) over monandry (see Chapter 3), which in turn is expected to impact sexual selection. In particular, higher female mating frequencies are expected to increase the relative strength of post-copulatory sexual selection but to reduce the total opportunity for, and strength of, sexual selection (Evans and Garcia-Gonzalez 2016), due to a reduction of the variance in male mating success as females' mating rates increase (Collet et al. 2012; McDonald et al. 2013; McDonald and Pizzari 2018). The bottom line is that both sexual selection and population spatial structure may have independent, but also interacting, important but so far neglected implications for the evolution of body size and SSD.

Here, we employ a novel 2x2 (mating system by population structure) experimental evolution setting to investigate, for the first time, the independent and interactive effects of mating system and spatial population structure on the evolution of body size and SSD. To this purpose, we use as study system de been beetle *Callosobruchus maculatus*, a polygamous species with sexual dimorphism (Savalli and Fox 1999) that exhibits intense sexual selection and conflict (Crudgington and Siva-Jothy 2000; Crudgington 2001; Rönn et al. 2007; Hotzy and Arnqvist 2009). Our approach provides a rare insight into the evolution of body size and SSD; the results suggest striking influences of mating system and population spatial structure on sex-specific patterns of body size evolution.

Material and methods

Details about the experimental evolution protocol are thoroughly described in Chapter 1. Body size measures included in this chapter were taken in adult males and females along the selection experiment. More precisely, the data were collected in generations 13, 18 and 32 for males and generations 12, 13, 18, 30, 32 and 47 for females. All the individuals were reared under common garden (see Chapter 1) before the measurements were taken; any divergence in body size can

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therefore be attributed to genetic effects due to variation in the selection regimes across treatments, rather than to parental effects or other environmental effects due to differences in the breeding regimes.

Elytron length (henceforth EL) was used as a proxy of body size (Cayetano 2010). This trait is easy to measure with very low measurement error. Repeatability of the measurements was calculated following Becker (1984) on a subset of individuals (N=316; 158 individuals/sex) that were measured twice. The repeatability of EL is significant and very high for both sexes (males: 0.928, females: 0.998; all p-values <0.0001).

EL measurements were carried out on pictures taken from individuals that were previously frozen. Images were taken using a stereomicroscope SteREO Discovery.V8 (Carl Zeiss Microscopy GmbH, Germany) connected to a camera AxioCam Icc 1 (Carl Zeiss, Germany). Measurements were taken on the images using the software ZEN 2 (blue edition, Carl Zeiss Microscopy GmbH, 2011). For the subset of individuals used in the calculations of repeatability the mean value of the two measurements per individual was used in the analyses below. Due to the high repeatability of the measurements, the rest of individuals were measured only once. EL was always measured on the right elytron of the individuals (Fig. 2.1).

Fig. 2.1. Measurement of elytron length. The image shows the dorsal view of a female *C. maculatus*. Elytron length (in millimeters) was always measured on the right elytron. The measurement was always carried out parallel to the edge and connecting the most distant points of the right wing.

A total of 1736 individuals (N = 664 males and 1072 females) were measured. The age of the experimental individuals when measured ranged from 2 to 5 days for males and from 2 to 42 days for females. The range of variation for female age was greater than for males because some of the measured females were used in mating and longevity assays and they could not be measured until the end of the assays. Nevertheless, with the exception of a few insect species the body length of the adult insect (imago) do not change with age(Sehnal 1985), and this is true for *Callosobruchus maculatus* too, and specially if a hard structure like the elytrum is measured.

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In addition to body size estimated through EL, we measured body weight, another measure of body size related to body condition (Peig and Green 2010; Wilder et al. 2016). In contrast to EL, the body weight of individual males and females *C. maculatus* may vary substantially along time, specially after mating interactions, because the weight of the ejaculate transferred to females is a large fraction of the weight of the adult male (e.g. Eady et al. 2007). Additionally, dehydration, among many other reasons, can be another source of variation regarding body weight. Finally, if body weight is measured on dead animals, variation can arise due to desiccation, which would be related to the length of the period from death to the measurement of the trait. For all these reasons, first, we preferred to focus on EL as a proxy of body size, and second, for our measures of body weight we measured fresh body weight of live virgin individuals and soon after adult emergence (when they were 1 day old). To this purpose, small groups of isolation microtubes containing the virgin individuals were placed for a couple of minutes on ice and once the animals stopped moving they were transferred to a laboratory chill table (model#1431, BioQuip products, USA) before weighing them in a microbalance (Sartorius Stedim Biotech Genius ME215S Electronic Analytical and Semi-Microbalance, Readability: 0.00001 g). Repeatability of body weight was calculated on two measures for each of 472 *C. maculatus* non-experimental females that were used for different purposes (repeatability > 0.99, p <0.0001). Due to the high repeatability of the trait, the focal individuals from the selection experiment were weighed only once. A total of 960 individuals (N = 320 individuals/sex at generation 45 and 160 individuals/sex at generation 46) were weighed. Individuals from generation 45 were not measured after common garden breeding, while individuals from generation 46 were measured after one generation of common garden. For individuals of generation 45 we also measured EL (at the time of death), but it was not possible to measure EL in animals from generation 46 because they were used in a subsequent experiment in which different groups of animals were housed together and we could thus not identify individuals at the time of death to relate EL to fresh body weight. The analysis relating these two traits is therefore restricted to animals from generation 45.

Statistical analyses

Our main data analysis followed a protocol to identify and exclude, *a priori*, influential observations and outliers. Observations that met both the criteria of being an influential observation determined by Cook's distance (Quinn and Keough 2002), and being an outlier determined by the mean ± 2 standard deviations rule (Miller 1991), were excluded from our main analysis. In total, for the EL dataset, 8 observations out of 672 for males and 23 observations out of 1095 for females met these criteria and were excluded; final sample sizes were therefore 664 males and 1072 females. For the body weight dataset, the final sample sizes for the analyses at generation 45 with EL as covariate were 312 males and 307 females, after excluding 2 and 4 "influential outlier" observations, respectively. For the model without EL as covariate none of the observations was an influential outlier and, in this analysis, all 314 males and 311 females measured at generation 45 were included. For the analysis on body weight variation at generation 46, the final sample sizes consisted of 160 males and 159 females, after excluding 1 female observation that met the influential outlier criteria. Our main analyses were therefore conservative. However, we also run confirmatory analyses including all

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data to assess whether the inclusion of what we called 'influential outliers' rendered qualitatively different results to those from the main analyses. Results were identical before and after the removal of influential outliers and we thus just show here the results of the main analyses. The data in our main analysis (i.e., excluding influential outliers) provided also a better fit to the basic assumptions of normality and homoscedasticity from linear models.

Divergence in the response of body size and SSD to the selection treatments was analyzed in R 3.3.2 (R Core Team 2016). First, we investigated the evolution of body size for each sex separately. Second, we examined evolutionary divergence in SSD, with data from generations 13, 18 and 32, for which we had information from both sexes. In all cases Linear Mixed Models (LMM) were fitted using the function '*lmer*' implemented within the package '*lme4*' (Bates et al. 2015). EL, untransformed and measured in millimeters, was the response variable. Mating system (fixed factor with two levels: monogamy or polyandry), population spatial structure (fixed factor with two levels: Non-structured populations or Structured populations (metapopulations)) and their interaction, as well as generation, were included as fixed factors. Sex (fixed factor with two levels: male or female) was additionally included in the analyses of the SSD. Selection line (see Chapter 1), from 1 to 16, was included in the models as a random factor. Selection lines are nested within each of the mating system x spatial structure combination (i.e., what we call "selection regimes": SPoly, SMono, NSPoly and NSMono; see Chapter 1).

We were interested in the contribution of particular effects to variance in the dependent variables (i.e. hypothesis testing) rather than on finding the best model out of many competing ones. In other words, the focus of our targeted and specific experimental design and analyses is to test the role of a few a priori relevant predictors in explaining variance in the response variable. Stepwise regression methods on such low number of predictors and therefore small amounts of model reduction is in general considered appropriate (see Pinheiro and Bates 2000; Bolker et al. 2009), and we thus adopted this approach. We followed the same protocol in all cases. First, we fitted the full model (the model with all the predictors and their interactions) and tested it against the null model (the model lacking the predictors of interest but including the random structure of the data, i.e., the random factor Selection Line) with a Likelihood Ratio Test (LRT) using the R function '*anova*' with argument test set to '*Chisq*'. It has been suggested that significance tests for individual predictors should only be considered once the full model reveals significance, unless an error-level adjustment for multiple testing is used to avoid inflation of Type-I error (Forstmeier and Schielzeth 2011). Despite our low number of predictors, we wanted to err on the conservative side and chose to minimize Type-I errors by adjusting p values for multiple testing using the Benjamini-Hochberg procedure (Benjamini and Hochberg 1995).

In the analysis of body size (EL) the full model included a three-way interaction among mating system, population spatial structure and generation, as well as all the possible pairwise interactions among these three factors. In the analysis of SSD the full model included the three-way interaction among mating system, population spatial structure and sex, and all the possible pairwise interactions among these three factors. Interactions among any of these factors and generation were not included in the analysis of SSD for several reasons. First, variation

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attributable to generation could in reality be, at least partially, error variation arising from the fact that measurements across generations were taken by different persons. EL measures are straightforward and highly repeatable, but still, some variation across generations could be the result of slightly different ways of taking the measurements by different observers (this does not affect the data within any given generation). Second, bean size changed along time (see Discussion), and bean size determines to a large extent the food available for the developing larva and so, it may presumably influence the size of the adult beetle emerging from it (again this is an issue that does not affect the analysis of within-generation variation).

We ran progressively simplified models by removing fixed effects (or their interactions) one-at-a-time using the '*drop1'* function (argument test set to '*Chi*') from the package '*stats*' (R Core Team 2016), and given our large sample sizes we tested the effect of removal of each term on the change in model deviance using LRT and maximum likelihood (Bolker et al. 2009). The final model included the significant effects (alpha criterion of 0.05), if any, and we also always retained in the final model the fixed factors mating system and structure plus the random factor selection Line, regardless of the contribution of these factors, to account for the structure of the experimental design and the hierarchical structure of the data (i.e., for the fact that the data is grouped by the random factor within each combination of mating system and population structure selection levels). The effects of non-significant terms were assessed at the end of the process through a LRT comparing the final model with and without the term.

While significance of the fixed effects was calculated using maximum likelihood as described above, parameter estimates of the fixed and random effects in the final model were calculated using Restricted Maximum Likelihood (REML), as it is suggested (Bolker et al. 2009; Zuur et al. 2009). The random effect was tested with a LRT, comparing the final Linear Mixed Model with the random term and a Linear Model without the random factor (Lynch and Walsh 1998; Bolker et al. 2009).

We report mean ± standard error values throughout. Tables are provided after the references. Parameter estimates and other details of the models run can be found in the Appendix at the end of the chapter.

Results

Divergence in body size

Males

There was a pattern for males evolving under a polygamous mating system to achieve a larger body size than those evolving under monogamy, as well as a pattern suggestive of interactive effects between the two selection regimes on male body size (Fig. 2.2a). However, none of the main effects or their interactions were significant, although the mating system effect and their interaction with the structure effect were marginally non-significant (Table 2.1).

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There was also a highly significant influence of generation (LRT = 336.65, df = 1, p<0.0001; Fig. 2.3a). We run the analysis for each generation separately (Table 2.2). These analyses inform that there is some variation in the way each factor contributes to male body size across generations, but the general pattern observed in the analysis including all generations is conserved (Fig. 2.4; Table 2.2). Table 2.9 shows the male body size means for each of the groups analyzed, both across and within generations and selection treatments.

Females

The effect of generation was, as for males, significant (Fig. 2.3b, Table 2.3). The interaction among generation, mating system and population spatial structure was statistically significant (LRT = 87.8, df = 1, p <0.0001). Fig. 2.2b shows the interactive effects of mating system and population spatial structure on female body size across generations. The analyses carried at the within-generation level show the existence of temporal variation in regards to the influence of the selection treatments along the selection experiment (Table 2.4, Fig. 2.5). Table 2.10 shows the female body size means for each of the groups analyzed, both across and within generations and selection treatments.

Evolution of sexual size dimorphism (SSD)

Remarkably, the multi-generation analysis of the evolution of differences in body size between males and females reveals that SSD depends on mating system, with males evolving a smaller, but females evolving a larger body size under a monogamous selection regime than under the intense sexual selection experienced by polygamous selection lines (Fig. 2.6).

The analysis reveals a striking sex-specific response to the selection regimes regarding body size evolution; in other words, the different evolutionary trajectories in body size evolution between the sexes leads in turn to the evolution of SSD (Fig 2.7). In polygamous populations female body size varies less along time than male body size (i.e., the slope of the relationship between body size and time under the polygamous selection regime is shallower for females than for males). However, in monogamous populations it is females the sex that exhibits a higher response to the selection regime (in this case release of sexual selection), and critically, under the absence of sexual selection and sexual conflict females attain larger sizes than their polygamous counterparts (see Figure 2.7). As a result of these sex-specific responses to the presence or absence of sexual selection, higher SSD is favoured under monogamy. This pattern, evidenced in Figure 2.7, is supported by the existence of a significant interaction between mating system and sex (Table 2.5).

We run additional analyses for each generation separately. The results were, however, not entirely consistent (Table 2.6). We believe that these differences may arise due to either measurement error (unlikely) or to differences in the way that changes in bean size across generations affect the potential to reach optimal size for each sex depending on treatment. Unfortunately, we did not measure directly variation in bean size and so we cannot explore the influence of this factor on adult size. For this reason, we retain ourselves from interpreting heterogeneity in the

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results at the whithin- generation level when assessing the evolution of SSD and focus instead on the general analysis across generations.

Divergence in body weight

Males

In the model of fresh body weight before a generation of common garden (generation 45) males evolving under a polygamous mating system were significantly heavier than their monogamous counterparts (LRT = 8.14, df = 1, p = 0.0043). Population spatial structure and its interaction with mating system did not explain body weight variation (Table 2.7). After common garden (generation 46), body weight was not influenced by either the main effects (mating system and spatial population structure) or their interaction (see Table 2.8). So, it seems variation in body weight is largely explained by parental/environmental effects rather than genetic effects shaped by the selection regimes. Moreover, unsurprisingly, body size (EL) explained to a large extent body mass, as inferred from a model run with animals on generation 45 in which we could include EL as a covariable: larger males are heavier (LRT = 258.95, df = 1, p <0.0001, Fig. 2.8a). But still, after accounting for the relationship between EL and body weight there is variation in body weight explained by mating system, with polygamous males being larger than monogamous males (LRT = 9.07, df = 1, p = 0.0026). As with the other models, population spatial structure and its interaction were not significant (Table 2.7). Table 2.11 shows the male body weight means for each of the groups analyzed, both across and within generations and selection treatments.

Females

As for males, the model before a generation of common garden (generation 45) indicated that females from the polygamous populations are heavier than those from monogamous lines (LRT = 8.13, df = 1, p = 0.0044). Similar to males, spatial population structure and its interaction with mating system did not explain body weight variation in females (Table 2.7). After common garden (generation 46), female body weight was not explained by either the main effects (mating system and spatial population structure) or their interaction (see Table 2.8). So, as it happens in males, variation in body weight seems to be explained at least in part by parental/environmental effects. Finally, as for males, the model with data from generation 45 including EL as a covariable indicates that body size (EL) explains female body mass, with larger females being heavier (LRT = 195.45, df = 1, p <0.0001, Fig. 2.8b). In this case, there is a signal for variation in body weight beyond that explained by EL to be explained by mating system, but the effect of this factor was marginally no significant in this model (LRT = 3.59, df = 1, p = 0.0579; polygamous females tending to be heavier than monogamous females). As in the other models, and as it is the case for males, population spatial structure and its interaction with mating system did not explain variation in body weight for females (see Table 2.8). Table 2.11 shows the female body weight means for each of the groups analyzed, both across and within generations and selection treatments.

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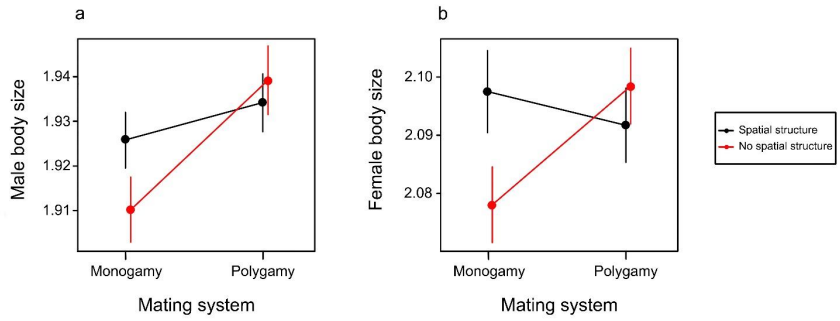

Fig. 2.2. Interactive effects of mating system (monogamy vs. polygamy) and population spatial structure (structure vs. no structure) on male (a) and female (b) body size (mean±1SE) across all generations examined. Red and black circles show the data for non-structured, and structured populations, respectively.

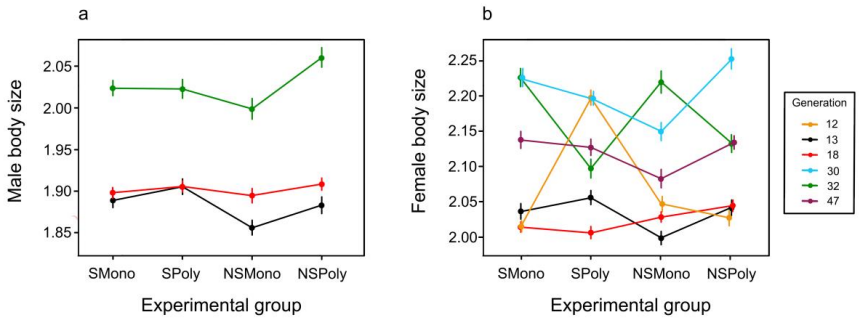

Fig 2.3. Variation in body size (in millimeters) per treatment for the different generations assayed, for males (a) and females (b). The graph shows means (circles) and SEs (bars).

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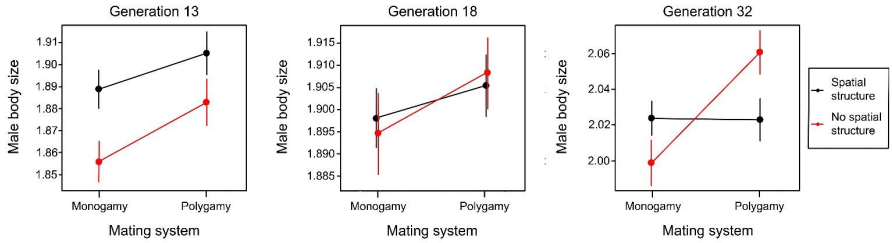

Fig. 2.4. Variation in the way mating system and spatial population structure influence male body size (in millimeters) in the different generations assayed. The graphs show the mean (circles) ± 1SE (bars). Red circles correspond to the values in the non-structured populations while black circles correspond to the values from structured populations.

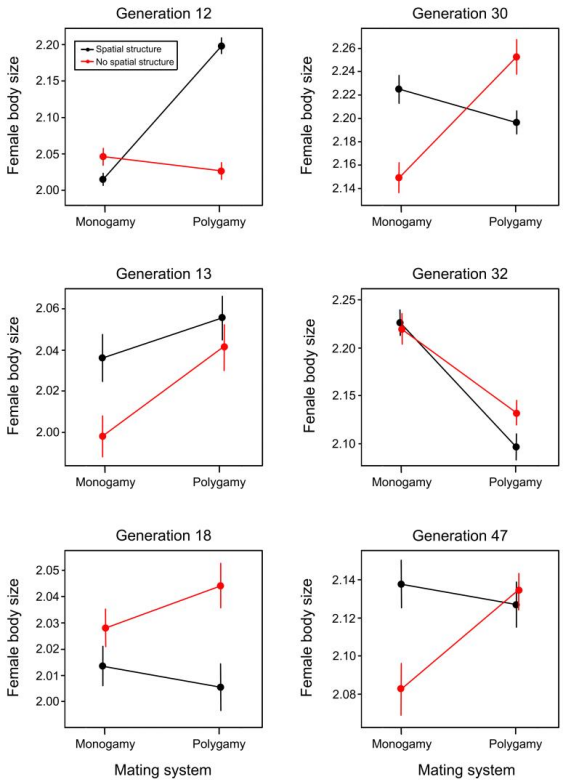

Fig. 2.5. Temporal fluctuations in the way mating system and spatial population structure explain female body size (in millimeters). The data show means ± 1SE. Red circles correspond to the values in the non-structured populations while black circles correspond to the values from structured populations.

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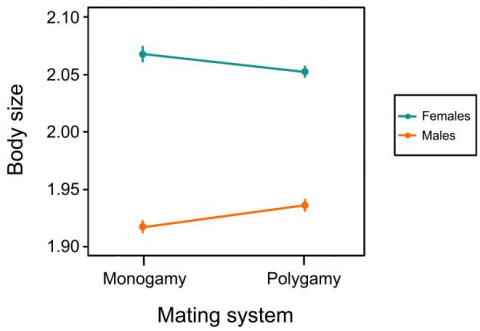

Fig. 2.6. The effect of mating system on sexual size dimorphism. The graph shows the mean ± 1SE body size (in millimeters) across all individuals in all generations assayed (see Methods), per sex and according to mating system selection regime. As it can be seen, the magnitude of SSD has increased under monogamy selection relative to SSD under intense sexual selection; this is due to a reduction, and an increase, in body size for males and females, respectively, when animals are released from sexual selection (i.e. under monogamous selection; see Discussion) (see also Figure 2.7).

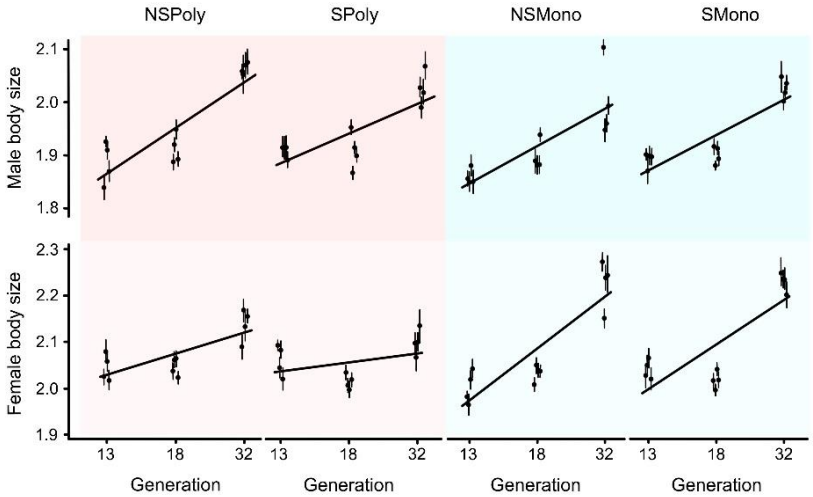

Fig. 2.7. The evolution of sexual size dimorphism (SSD) in *Callosobruchus maculatus*. The figure shows sex-specific evolutionary trajectories in body size responses to the selection regimes. Male body size variation is depicted in the upper region of the graph and female body size variation in the lower region, and data for the four selection regimes determined by the combination of selection treatments are shown. Means (circles) and SEs (bars) of data for each replicate line are depicted. In the polygamous populations (red shadow) the male response regarding the evolution of the body size across generations is of higher

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magnitude (steeper slope) than the female response. In monogamous populations (blue shadow), however, both sexes have a more similar response, with females presenting a slightly steeper slope. Consequently, in polygamous populations SSD is reduced (males increase in size while females remain more static) while in monogamous populations SSD increases, due to a higher increase in female body size compared to males when individuals are released from sexual selection and sexual conflict. Males present a similar response across selection regimes, but the female response varies according to mating system. In absence of sexual selection and sexual conflict (monogamy) female body size evolves towards higher values than under intense sexual selection and sexual conflict.

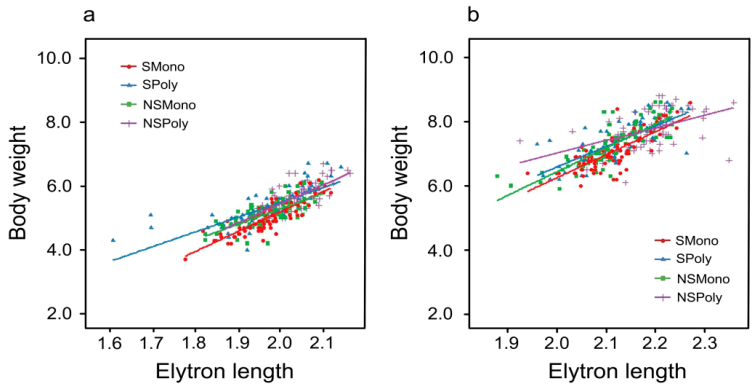

Fig. 2.8. Relationship between body weight (in milligrams) and body size (in millimeters) for males (a) and females (b) of the selection regimes resulting from the combination of mating system and population spatial structure.

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Discussion

Body size is a critical trait with key life-history implications (LaBarbera 1989; Blanckenhorn 2000; Chown and Gaston 2010), but despite its relevance many questions regarding its evolution remain unsolved. Sexual size dimorphism is a widespread phenomenon in nature (e.g. Fairbairn 1997; Székely et al. 2000; Fox and Czesak 2006; Fairbairn et al. 2007; Lindenfors et al. 2007) and its direction and magnitude vary among species and even among populations within species (Blanckenhorn et al. 2006; Blanckenhorn 2007). Male-biased SSD, where males are larger than females, is present in most mammal and bird species while female-biased SSD, when females are distinctively larger than males, is the common pattern in most invertebrate groups (Zamudio 1998; Blanckenhorn 2005; Fairbairn et al. 2007), and it is also the case in the seed beetle *C. maculatus*. SSD results from the equilibrium among the selection pressures acting on body size in males and females, as well as the constraints imposed by several genetic, ecological, developmental and physiological factors (Shine 1989; Delph 2005; Fairbairn et al. 2007; Stillwell et al. 2010).

The principal aim of this chapter was to evaluate the evolution of body size and SSD in response to sexual selection and to selection arising from variation in population spatial structure, as well as from the interaction between these two selection forces. A remarkable sex-specific response regarding the evolution of the body size to the presence/absence of sexual selection was detected: in polygamous populations SSD is reduced (males increase in size while females remain more static) while in monogamous populations SSD increases, due to a higher increase in female body size compared to males when individuals are released from sexual selection and sexual conflict.

The results above were obtained in analyses focusing on a linear dimension, elytron length, which is invariable with respect to age or body condition in insects. Body mass is also sometimes used as a measure of body size in insects (Kaspari and Weiser 1999). In our study, body mass was positively and strongly correlated with elytron length. Males evolving under a polygamous mating system were significantly heavier than males from the monogamous populations. Interestingly, controlling for the influence of body length on an individual's body weight, mating system still explained variation in body mass, with males from polygamous populations being heavier than their monogamous counterparts. It thus may seem that sexual selection selects for higher body condition in male *C. maculatus*, a pattern found in other studies (e.g. Simmons and Garcia-Gonzalez 2008). However, the effect of mating system on divergence in body mass disappeared when the analysis was carried after one generation of common garden. This suggests that the effect of mating system on body mass is mainly driven by parental and/or other environmental effects due to the breeding (e.g., multiple mating in the polygamous lines vs. single mating in the monogamous populations) rather than by selection arising from the selection regime. This may include benefits accrued by females only when they mate multiply (or female differential allocation) that could result in the production of larger offspring.

The reasons underlying the fluctuations that we have detected in the analyses of body size evolution across generations are difficult to be assessed, due to several

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potential sources of variation in addition to the selection agents that we imposed in our experiment. First, temporal variation may be partly explained by measurement errors since the trait measurements in different generations were taken by different persons. These persons were trained with a subsample of individuals so that the traits were always measured following the exact same protocol, but we cannot exclude completely the possibility that some of the variation in the data may be originated from slight variation due to the observer identity. Second, variation in bean size across generations might be another important factor. In this species egg to adult development occurs inside a seed, and the resources available for the development depend greatly on seed size (Fox et al. 2007). We are aware that the size of the beans in our selection experiment if anything slightly declined with time. For instance, the number of beans in a standard volume of beans allocated to a small plastic container in 2014 was lower (319.67±1.54 beans, n = 3 standard containers) than in 2018 (334.33±1.02 beans, n = 3 standard containers). However, despite a slight decrease in bean size along time, the size of the individuals across all selection regimes increased with time. Therefore, variation in bean size is unlikely to explain the temporal variation in body size and SSD that we have documented here. Moreover, even within a given generation, in which individuals from the different selection lines are exposed to beans of similar size, differences in the size of individuals and sexes were observed depending on the selection regimes, which again speaks of a negligible influence of bean size variation on the patterns of divergence in body size in our study.

Sexual selection has been suggested as one the major evolutionary forces underlying the evolution of body size. Under polygamy, males must be able to outcompete potential rivals to get access to females. Under such conditions, larger male body size would be associated to higher male reproductive success (Parker 1979; Andersson 1994; Blanckenhorn 2000; Moore et al. 2009). Additionally, large male body size is frequently also favoured by female choice (Simmons 1987; Andersson 1994; Blanckenhorn et al. 2000). This is unsurprising if body size is heritable and determines male reproductive success (e.g., through male-male competition), because females mating with larger males would produce larger and successful offspring. In other cases, larger males may be preferred by females because they increase female fecundity via larger nuptial gifts (Fox et al. 2006).

Sexual conflict, or the differences in the evolutionary interests of males and females (Parker 1979; Arnqvist and Rowe 2005) may also shape the evolution of body size. *C. maculatus* is a model species for the study of sexual conflict. In this species, copulation imposes longevity costs to females as a consequence of injuries caused by the males' spiny genitalia (Crudgington and Siva-Jothy 2000). Seminal fluid proteins may also play a role on sexual conflict in this species (Yamane et al. 2015), as it does in other species (Chapman et al. 1995; Chapman and Davies 2004; Yamane 2013). Females of this species exhibit several traits that seem to have evolved as counter adaptations to male harm, for instance, kicking behaviour by which females kick the male during the last third of the mating events in order to shorten copulation (Crudgington and Siva-Jothy 2000; Crudgington 2001; van Lieshout et al. 2014; but see Wilson and Tomkins 2014), or thick walls of the reproductive tract to ameliorate the damage inflicted by genital spines (Rönn et al. 2007; but see Dougherty and Simmons 2017). Both sexes are thus believed to be in a race for the control over copulation and mating interactions (Crudgington 2001;

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Edvardsson and Tregenza 2005; Edvardsson and Canal 2006; van Lieshout et al. 2014; Wilson and Tomkins 2014), and body size may play a crucial role in this regard. From the male perspective, a larger body size may facilitate to hinder taking over attempts by rival males and may help to gain control over the duration of copulation. Moreover, larger males transfer larger ejaculates (Savalli and Fox 1998), and in this species, as in others, the compounds in the ejaculate modify female reproductive behaviors (e.g. Eady 1995; Fox et al. 2006; Yamane et al. 2008; Yamane and Miyatake 2010a, c, b; Yamane et al. 2015). However, the role of male size on male fitness in this species has been questioned (Savalli and Fox 1999; Fox et al. 2007).

From a female perspective, a larger body size would presumably facilitate resisting mating attempts and to dislodge mating males, if this is in the benefit of the female. Additionally, fecundity selection has been pointed out as another major selective force acting on body size evolution, pushing females towards larger body sizes (Blanckenhorn 2000). Larger females generally have greater fecundity and produce larger offspring (Stillwell et al. 2010 and references therein). In fact, our results unveil a connection between these two forces (sexual selection/conflict and fecundity selection) driving the evolution of female body size and by extension SSD. A previous study in *Callosobruchus chinensis* has suggested that the costs derived from male harassment could be higher than the costs accrued through multiple mating, and therefore that it could be less harmful for females to remate than to reject mating attempts continuously (Harano 2015). With that in mind a possible explanation to the steeper response of female body size under monogamy selection could be attributed to a release from the costs of sexual conflict. Females from monogamous lines would have been released from paying the high costs of sexual conflict, or from investment in counter adaptations to male harm, and this may in turn would had allowed females to respond to fecundity selection, devoting resources to increase offspring number or offspring quality (e.g., through increases in egg size). The shallower response in female body size to the presence of sexual selection (polygamous populations) would be the other side of the coin: these females are not expected to respond to fecundity selection because of the above mentioned costs of harassment, and because females in the polygamous populations are expected to develop resistance traits to male persistence traits (e.g. Holland and Rice 1999; Arnqvist and Rowe 2005; Dougherty et al. 2017), which would trade-off with other biological functions (e.g. Eady and Brown 2017), probably limiting the ability of females to respond to fecundity selection.

In conclusion, we have not found evidence for selection arising from variation in population spatial structure to influence the evolution of body size and SDD, at least under the experimental conditions established. However, our data shows that sexual selection and mating system underlie the evolution and maintenance of SSD in unexpected ways due to sex-specific selection. Intense sexual selection and sexual conflict leads to responses in the sexes that altogether imply a reduction in SSD, while the removal of sexual selection and the release of costs arising from sexual conflict leads to evolutionary responses in the sexes that ultimately imply an increase in SSD.

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Table 2.1. Analysis of male body size across generations 13, 18 and 32. The expression 'mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal $R^2 = 0.39$; conditional $R^2 = 0.42$.

Effect	LRT	p
Mating system : structure : generation	4.93	0.09
Mating system : generation	2.47	0.29
Structure:generation	5.55	0.06
Mating system : structure	1.35	0.24
Mating system	3.20	0.07
Structure	0.28	0.60
Generation	336.65	**<0.0001**
Line (Random)	14.33	**0.0002**

Table 2.2. Analysis of male body size per generation. The expression 'mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text).

Effect	Gen 13		Gen 18		Gen 32	
	LRT	p	LRT	p	LRT	p
Mating system : structure	0.29	0.59	0.08	0.78	2.92	0.09
Mating system	4.19	0.0408	0.71	0.40	2.33	0.13
Structure	6.46	**0.011**	0.001	0.98	0.11	0.74
Line (Random)	0.05	0.83	9.46	**0.002**	12.84	**0.0003**

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Table 2.3. Analysis of female body size across generations 12, 13, 18, 30, 32 and 47. The expression 'mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal $R^2 = 0.54$; conditional $R^2 = 0.55$.

Effect	LRT	p
Mating system : structure : generation	87.80	**<0.0001**
Mating system : generation	118.80	**<0.0001**
Structure : generation	41.38	**<0.0001**
Mating system : structure	3.04	0.08
Mating system	0.85	0.36
Structure	0.65	0.42
Generation	584.57	**<0.0001**
Line (Random)	6.91	**0.0086**

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Table 2.4. Analysis of female body size per generation. The expression 'mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text).

Effect	Gen 12		Gen 13		Gen 18		Gen 30		Gen 32		Gen 47	
	LRT	p	LRT	p	LRT	p	LRT	p	LRT	p	LRT	p
Mating system : structure	31.49	**<0.0001**	0.79	0.37	2.21	0.14	13.65	**0.0002**	1.74	0.19	2.57	0.11
Mating system	7.03	**0.0081**	4.69	0.03	0.25	0.62	2.76	0.09	21.54	**<0.0001**	0.90	0.34
Structure	5.57	**0.0183**	3.49	0.06	7.64	**0.0057**	0.21	0.65	0.87	0.35	1.27	0.26
Line (Random)	0	1	2.06	0.15	0.05	0.82	0.67	0.41	0.93	0.34	18.84	0.26

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Table 2.5. Analysis of the evolution of SSD across generations 13, 18 and 32. The expression 'mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal R^2= 0.58; conditional R^2= 0.59.

Effect	LRT	p
Mating system : structure : sex	5.09	0.17
Mating system : sex	16.48	**<0.0001**
Structure : sex	2.73	0.09
Mating system : structure	2.32	0.13
Mating system	0.02	0.88
Structure	0.05	0.83
Sex	757.66	**<0.0001**
Line (Random)	21.35	**<0.0001**

Table 2.6. Analysis of SSD per generation. The expression 'mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text).

Effect	Gen 13		Gen 18		Gen 32	
	LRT	p	LRT	p	LRT	p
Mating system : structure : sex	1.41	0.84	1.03	0.79	3.51	0.32
Mating system : sex	0.48	0.49	0.26	0.61	59.30	**<0.0001**
Structure : sex	0.01	0.93	4.69	0.03	0.32	0.57
Mating system : structure	0.71	0.40	0.49	0.49	2.83	0.09
Mating system	5.56	**0.018**	0.73	0.39	4.92	0.03
Structure	5.85	0.0155	1.48	0.22	0.46	0.49
Sex	277.22	**<0.0001**	371.33	**<0.0001**	166.34	**<0.0001**
Line (Random)	5.315	**0.0211**	10.99	**0.0009**	17.88	**<0.0001**

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Table 2.7. Analysis of male and female body mass after 45 generations of evolution. The expression 'mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: males (without EL: marginal R^2= 0.17, conditional R^2= 0.34; with EL: marginal R^2= 0.67, conditional R^2= 0.73), females (without EL: marginal R^2= 0.19, conditional R^2= 0.38; with EL: marginal R^2= 0.57, conditional R^2= 0.59).

Analysis with elytron length as covariate				
Effect	**MALES**		**FEMALES**	
	LRT	**p**	**LRT**	**p**
Mating system : structure	1.13	0.28	3.36	0.07
Mating system	9.07	**0.0026**	3.60	0.0579
Structure	0.42	0.52	2.05	0.15
Elytron length	258.95	**<0.0001**	195.45	**<0.0001**
Line (Random)	32.27	**<0.0001**	3.72	0.0536
Analysis without elytron length as covariate				
Effect	**LRT**	**p**	**LRT**	**p**
Mating system : structure	0.56	0.45	0.33	0.56
Mating system	8.14	**0.0043**	7.31	**0.0068**
Structure	2.49	0.11	3.79	0.0516
Line (Random)	43.65	**<0.0001**	23.10	**<0.0001**

Table 2.8. Analysis of male and female body mass after 46 generations of evolution. This analysis was carried out after one generation under common garden. The expression 'mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: males (marginal R^2= 0.09; conditional R^2= 0.30), females (marginal R^2= 0.07; conditional R^2= 0.33).

Effect	**MALES**		**FEMALES**	
	LRT	**p**	**LRT**	**p**
Mating system : structure	1.54	0.21	0.59	0.44
Mating system	3.50	0.06	1.37	0.24
Structure	0.83	0.36	1.86	0.17
Line (Random)	23.9	**<0.0001**	27.08	**<0.0001**

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Table 2.9. Means ± 1 SE and sample size (within brackets) of male body size (in millimeters) for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). These individuals were included in the analysis of sexual size dimorphism.

Generation	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Generations 13-32 combined	1.93 ± 0.0063 (168)	1.93 ± 0.0065 (163)	1.91 ± 0.0073 (167)	1.94 ± 0.0079 (166)	1.92 ± 0.0049 (325)	1.94 ± 0.0051 (329)	1.93 ± 0.0045 (331)	1.92 ± 0.0054 (333)
13	1.89 ± 0.0088 (40)	1.91 ± 0.0097 (37)	1.86 ± 0.0094 (40)	1.88 ± 0.0105 (38)	1.87 ± 0.0066 (80)	1.89 ± 0.0072 (75)	1.90 ± 0.0066 (77)	1.87 ± 0.0071 (78)
18	1.90 ± 0.0067 (88)	1.91 ± 0.0070 (86)	1.91 ± 0.0070 (87)	1.91 ± 0.0080 (88)	1.90 ± 0.0057 (175)	1.91 ± 0.0053 (174)	1.90 ± 0.0048 (174)	1.90 ± 0.0061 (175)
32	2.02 ± 0.0096 (40)	2.02 ± 0.0120 (40)	1.99 ± 0.0130 (40)	2.06 ± 0.0124 (40)	2.01 ± 0.0082 (80)	2.04 ± 0.0088 (80)	2.02 ± 0.0076 (80)	2.03 ± 0.0096 (80)

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Table 2.10. Means ± 1 SE and sample size (within brackets) of female body size (in milimeters) for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). Females from generations 13, 18 and 32 were included in the analysis of sexual size dimorphism.

Generation	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Generations 12-47 combined	2.10 ± 0.0071 (271)	2.10 ± 0.0064 (266)	2.08 ± 0.0065 (265)	2.10 ± 0.0065 (270)	2.09 ± 0.0048 (536)	2.10 ± 0.0046 (536)	2.09 ± 0.0048 (537)	2.09 ± 0.0046 (535)
12	2.01 ± 0.0086 (27)	2.20 ± 0.01 (28)	2.05 ± 0.01 (28)	2.03 ± 0.01 (27)	2.03 ± 0.0076 (55)	2.11 ± 0.01 (55)	2.11 ± 0.01 (55)	2.04 ± 0.0083 (55)
13	2.04 ± 0.01 (40)	2.06 ± 0.01 (40)	1.99 ± 0.01 (39)	2.04 ± 0.01 (39)	2.02 ± 0.0079 (79)	2.05 ± 0.0077 (79)	2.05 ± 0.0078 (80)	2.02 ± 0.0079 (78)
18	2.01 ± 0.0076 (85)	2.00 ± 0.0090 (83)	2.03 ± 0.0076 (85)	2.04 ± 0.0085 (85)	2.02 ± 0.0054 (170)	2.03 ± 0.0063 (168)	2.00 ± 0.0058 (168)	2.04 ± 0.0057 (170)
30	2.22 ± 0.01 (40)	2.20 ± 0.0099 (39)	2.15 ± 0.01 (38)	2.25 ± 0.01 (39)	2.19 ± 0.0098 (78)	2.22 ± 0.0095 (78)	2.21 ± 0.0079 (79)	2.20 ± 0.01 (77)
32	2.23 ± 0.01 (40)	2.10 ± 0.0 (38)	2.22 ± 0.02 (38)	2.13 ± 0.01 (40)	2.22 ± 0.01 (78)	2.11 ± 0.0097 (78)	2.16 ± 0.01 (78)	2.18 ± 0.01 (78)
47	2.14 ± 0.01 (39)	2.13 ± 0.01 (38)	2.08 ± 0.01 (37)	2.13 ± 0.0098 (40)	2.11 ± 0.0097 (76)	2.13 ± 0.0077 (78)	2.13 ± 0.0086 (77)	2.11 ± 0.0088 (77)

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Table 2.11. Means ± 1 SE and sample size (within brackets) of male and female body weight (in milligrams) for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). [a] Sample sizes for models at generation 45 without including EL as covariate.

Sex	Generation	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Males	45 a	5.03 ± 0.06 (78)	5.36 ± 0.06 (79)	5.15 ± 0.05 (79)	5.66 ± 0.05 (76)	5.09 ± 0.04 (157)	5.51 ± 0.04 (155)	5.20 ± 0.04 (157)	5.40 ± 0.04 (155)
	b	(78)	(79)	(79)	(78)	(157)	(157)	(157)	(157)
	46 (after common garden)	5.53 ± 0.08 (40)	5.65 ± 0.11 (40)	5.48 ± 0.08 (40)	5.98 ± 0.09 (40)	5.51 ± 0.06 (80)	5.82 ± 0.07 (80)	5.59 ± 0.07 (80)	5.73 ± 0.07 (80)
Females	45 a	7.08 ± 0.07 (78)	7.41 ± 0.07 (74)	7.27 ± 0.07 (80)	7.76 ± 0.07 (75)	7.18 ± 0.05 (158)	7.59 ± 0.05 (149)	7.24 ± 0.05 (152)	7.51 ± 0.05 (155)
	b	(78)	(76)	(80)	(77)	(158)	(153)	(154)	(157)
	46 (after common garden)	7.45 ± 0.10 (40)	7.53 ± 0.13 (39)	7.58 ± 0.11 (40)	7.98± 0.10 (40)	7.51 ± 0.07 (80)	7.75 ± 0.09 (79)	7.49 ± 0.08 (79)	7.78 ± 0.08 (80)

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Appendix Chapter 2

Model: Evolution of male body size (across generations)

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod].Formula: elytrum ~ ss + structure + ss:structure + ss:gen +
structure:gen +  ss:structure:gen + gen + (1 | line)

     AIC      BIC   logLik deviance df.resid

 -1631.8  -1568.9    829.9  -1659.8      650
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.8879 -0.6018 -0.0204  0.6225  3.2128
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0002124 0.01457
 Residual             0.0046863 0.06846
Number of obs: 664, groups:  line, 16
Fixed effects:
                            Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                 1.888750   0.013048  67.900000 144.749   <2e-16 ***
sspoly                      0.015940   0.018710  71.500000   0.852   0.3971
structurenometa            -0.032875   0.018453  67.900000  -1.782   0.0793 .
gen18                       0.009318   0.013054 648.000000   0.714   0.4756
gen32                       0.134975   0.015307 648.000000   8.818   <2e-16 ***
sspoly:structurenometa      0.010964   0.026397  70.900000   0.415   0.6791
sspoly:gen18               -0.008869   0.018751 648.000000  -0.473   0.6364
sspoly:gen32               -0.016892   0.021867 648.000000  -0.772   0.4401
structurenometa:gen18       0.029378   0.018478 648.000000   1.590   0.1124
structurenometa:gen32       0.007800   0.021648 648.000000   0.360   0.7187
sspoly:structurenometa:gen18  -0.004482   0.026443 648.000000  -0.169   0.8655
sspoly:structurenometa:gen32   0.052000   0.030871 648.000000   1.684   0.0926 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + gen + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -1631.5  -1600.0    822.8  -1645.5      657

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.7287 -0.6196 -0.0211  0.6531  3.1229
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0002393 0.01547
 Residual             0.0047808 0.06914
Number of obs: 664, groups:  line, 16
Fixed effects:
                  Estimate Std. Error         df t value Pr(>|t|)
(Intercept)       1.876502   0.009469  28.900000 198.171   <2e-16 ***
sspoly            0.017750   0.009414  15.900000   1.885   0.0777 .
structurenometa  -0.004988   0.009414  15.900000  -0.530   0.6035
gen18             0.018592   0.006675 648.000000   2.785   0.0055 **
gen32             0.143570   0.007793 648.000000  18.422   <2e-16 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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Generation 13

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure + (1 |
line)

     AIC      BIC   logLik deviance df.resid

  -425.6   -407.4    218.8   -437.6      149
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.42154 -0.56502 -0.03717  0.67707  2.14289
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0000223 0.004722
 Residual             0.0034567 0.058794
Number of obs: 155, groups:  line, 16
Fixed effects:
                       Estimate Std. Error        df t value Pr(>|t|)
(Intercept)            1.888750   0.009591 14.616000 196.925   <2e-16 ***
sspoly                 0.016375   0.013820 15.727000   1.185   0.2537
structurenometa       -0.032875   0.013564 14.616000  -2.424   0.0289 *
sspoly:structurenometa  0.010479   0.019482 15.521000   0.538   0.5983
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by REML
t-tests use  Satterthwaite approximations to degrees of freedom ['lmerMod'].Formula: ely
trum ~ ss + structure + (1 | line)
REML criterion at convergence: -414

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.31302 -0.50324 -0.06381  0.64571  2.10513
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000122 0.01104
 Residual             0.003454 0.05877
Number of obs: 155, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)      1.886214   0.009399 12.303000 200.682   <2e-16 ***
sspoly           0.021566   0.010943 12.710000   1.971   0.0709 .
structurenometa -0.027802   0.010940 12.682000  -2.541   0.0250 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Generation 18

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -837.9   -814.8    424.9   -849.9      343
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.7777 -0.6375 -0.0084  0.5903  3.1041
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0003592 0.01895
 Residual             0.0049083 0.07006
Number of obs: 349, groups:  line, 16
Fixed effects:
                       Estimate Std. Error        df t value Pr(>|t|)
(Intercept)            1.898068   0.012066 15.884000 157.312   <2e-16 ***
sspoly                 0.006920   0.017102 16.027000   0.405    0.691
structurenometa       -0.003705   0.017083 15.955000  -0.217    0.831
sspoly:structurenometa  0.006841   0.024172 15.991000   0.283    0.781
```


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```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -839.8   -820.5    424.9   -849.8      344
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.7866 -0.6463 -0.0040  0.5808  3.1129
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0003619 0.01902
 Residual             0.0049084 0.07006
Number of obs: 349, groups:  line, 16
Fixed effects:
                   Estimate Std. Error         df t value Pr(>|t|)
(Intercept)      1.8963633  0.0104792 15.9080000 180.965   <2e-16 ***
sspoly           0.0103443  0.0121139 15.9790000   0.854    0.406
structurenometa -0.0002875  0.0121139 15.9790000  -0.024    0.981
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Generation 32

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -376.1   -357.6    194.0   -388.1      154
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.65860 -0.69353  0.04499  0.74904  2.27506
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0007671 0.02770
 Residual             0.0047006 0.06856
Number of obs: 160, groups:  line, 16
Fixed effects:
                         Estimate Std. Error         df t value Pr(>|t|)
(Intercept)             2.0237250  0.0175869 16.0000000 115.070   <2e-16 ***
sspoly                 -0.0009513  0.0248716 16.0000000  -0.038   0.9700
structurenometa        -0.0250750  0.0248716 16.0000000  -1.008   0.3284
sspoly:structurenometa  0.0629638  0.0351737 16.0000000   1.790   0.0924 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -375.1   -359.8    192.6   -385.1      155
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.57491 -0.70490  0.07482  0.72076  2.21022
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.001015 0.03186
 Residual             0.004701 0.06856
Number of obs: 160, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)      2.007984   0.016686 16.000000 120.337   <2e-16 ***
sspoly           0.030531   0.019268 16.000000   1.585    0.133
structurenometa  0.006407   0.019268 16.000000   0.333    0.744
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
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Model: Evolution of female body size (across generations)

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
  degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure + ss:gen + structur
e:gen +  ss:structure:gen + gen + (1 | line)

     AIC      BIC   logLik deviance df.resid
 -2489.2  -2359.8   1270.6  -2541.2     1046
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.9388 -0.6824  0.0313  0.7321  2.6965
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0001004 0.01002
 Residual             0.0054048 0.07352
Number of obs: 1072, groups:  line, 16
Fixed effects:
                              Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                  2.015e+00  1.501e-02  3.214e+02 134.226  < 2e-16 ***
sspoly                       1.828e-01  2.106e-02  3.139e+02   8.682 2.22e-16 ***
structurenometa              3.122e-02  2.106e-02  3.139e+02   1.483 0.139210
gen13                        2.115e-02  1.831e-02  1.056e+03   1.155 0.248423
gen18                       -1.215e-03  1.624e-02  1.056e+03  -0.075 0.940385
gen30                        2.100e-01  1.831e-02  1.056e+03  11.468  < 2e-16 ***
gen32                        2.112e-01  1.831e-02  1.056e+03  11.531  < 2e-16 ***
gen47                        1.232e-01  1.841e-02  1.057e+03   6.695 3.50e-11 ***
sspoly:structurenometa      -2.028e-01  2.978e-02  3.139e+02  -6.811 4.95e-11 ***
sspoly:gen13                -1.633e-01  2.576e-02  1.056e+03  -6.341 3.38e-10 ***
sspoly:gen18                -1.910e-01  2.285e-02  1.056e+03  -8.361 2.22e-16 ***
sspoly:gen30                -2.110e-01  2.583e-02  1.056e+03  -8.170 8.88e-16 ***
sspoly:gen32                -3.121e-01  2.590e-02  1.056e+03 -12.050  < 2e-16 ***
sspoly:gen47                -1.939e-01  2.596e-02  1.056e+03  -7.469 1.69e-13 ***
structurenometa:gen13       -6.927e-02  2.583e-02  1.056e+03  -2.682 0.007426 **
structurenometa:gen18       -1.740e-02  2.281e-02  1.056e+03  -0.762 0.445944
structurenometa:gen30       -1.067e-01  2.590e-02  1.056e+03  -4.122 4.05e-05 ***
structurenometa:gen32       -3.714e-02  2.590e-02  1.056e+03  -1.434 0.151788
structurenometa:gen47       -8.685e-02  2.604e-02  1.057e+03  -3.335 0.000881 ***
sspoly:structurenometa:gen13  2.264e-01  3.652e-02  1.056e+03   6.198 8.16e-10 ***
sspoly:structurenometa:gen18  2.276e-01  3.229e-02  1.056e+03   7.051 3.21e-12 ***
sspoly:structurenometa:gen30  3.341e-01  3.662e-02  1.056e+03   9.123  < 2e-16 ***
sspoly:structurenometa:gen32  2.443e-01  3.662e-02  1.056e+03   6.672 4.07e-11 ***
sspoly:structurenometa:gen47  2.653e-01  3.673e-02  1.056e+03   7.225 9.57e-13 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model: Identical values than full model

Model: Evolution of female body size (per generations)

Generation 12

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure +ss:structure + (1|line)
     AIC      BIC   logLik deviance df.resid
  -309.6   -293.4    160.8   -321.6      104
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.63260 -0.70976  0.04138  0.66531  2.47661
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000000 0.0000
 Residual             0.003147 0.0561
```


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```
Number of obs: 110, groups:  line, 16
Fixed effects:
                       Estimate Std. Error        df t value Pr(>|t|)
(Intercept)             2.01481    0.01080 110.00000 186.631  < 2e-16 ***
sspoly                  0.18286    0.01513 110.00000  12.086  < 2e-16 ***
structurenometa         0.03126    0.01513 110.00000   2.066   0.0412 *
sspoly:structurenometa -0.20264    0.02140 110.00000  -9.470 6.66e-16 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model: Identical values than full model

Generation 13

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure +(1|line)
     AIC      BIC   logLik deviance df.resid
  -394.1   -375.7    203.0   -406.1      152
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.5750 -0.6643  0.0260  0.7619  2.2368
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000249 0.01578
 Residual             0.004280 0.06542
Number of obs: 158, groups:  line, 16
Fixed effects:
                       Estimate Std. Error       df t value Pr(>|t|)
(Intercept)             2.03600    0.01301 15.66900 156.500   <2e-16 ***
sspoly                  0.01950    0.01840 15.66900   1.060   0.3053
structurenometa        -0.03813    0.01847 15.91800  -2.064   0.0557 .
sspoly:structurenometa  0.02360    0.02613 15.91800   0.903   0.3799
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -395.3   -380.0    202.6   -405.3      153
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.51153 -0.64496 -0.02518  0.78104  2.27549
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0002832 0.01683
 Residual             0.0042802 0.06542
Number of obs: 158, groups:  line, 16
Fixed effects:
                Estimate Std. Error       df t value Pr(>|t|)
(Intercept)      2.03014    0.01156 15.73300 175.569   <2e-16 ***
sspoly           0.03121    0.01339 15.89000   2.332   0.0332 *
structurenometa -0.02635    0.01339 15.89400  -1.968   0.0667 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Generation 18

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure +(1|line)
     AIC      BIC   logLik deviance df.resid
  -781.5   -758.5    396.7   -793.5      332
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.8817 -0.6029  0.0307  0.7218  2.8178
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 8.458e-21 9.197e-11
 Residual             5.598e-03 7.482e-02
```


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```
Number of obs: 338, groups:  line, 16
Fixed effects:
                        Estimate Std. Error         df t value Pr(>|t|)
(Intercept)             2.013471   0.008115 338.000000 248.109   <2e-16 ***
sspoly                 -0.008049   0.011546 338.000000  -0.697    0.486
structurenometa         0.014235   0.011477 338.000000   1.240    0.216
sspoly:structurenometa  0.024519   0.016279 338.000000   1.506    0.133
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -781.2   -762.1    395.6   -791.2      333
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.9623 -0.6149  0.0479  0.6827  2.8652
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 2.216e-05 0.004708
 Residual             5.613e-03 0.074922
Number of obs: 338, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)      2.007392   0.007334 16.454000 273.713  < 2e-16 ***
sspoly           0.004271   0.008484 16.555000   0.503  0.62132
structurenometa  0.026428   0.008484 16.555000   3.115  0.00646 **
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Generation 30

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure +(1|line)
     AIC      BIC   logLik deviance df.resid
  -343.1   -324.8    177.5   -355.1      150
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.53380 -0.76304  0.04383  0.73962  2.32764
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0002015 0.01419
 Residual             0.0058349 0.07639
Number of obs: 156, groups:  line, 16
Fixed effects:
                      Estimate Std. Error       df t value Pr(>|t|)
(Intercept)            2.22486    0.01401 15.63600 158.823  < 2e-16 ***
sspoly                -0.02809    0.01991 15.92300  -1.411 0.177524
structurenometa       -0.07548    0.02001 16.23600  -3.773 0.001628 **
sspoly:structurenometa  0.13132    0.02829 16.22400   4.642 0.000262 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model: Identical values than full model

Generation 32

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure +(1|line)
     AIC      BIC   logLik deviance df.resid
  -308.7   -290.4    160.3   -320.7      150
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.68633 -0.71404  0.05764  0.70988  2.06776
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000199 0.01411
 Residual             0.007315 0.08553
```


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```
Number of obs: 156, groups:  line, 16
Fixed effects:
                       Estimate Std. Error        df t value Pr(>|t|)
(Intercept)             2.226013   0.015253 15.287000 145.941  < 2e-16 ***
sspoly                 -0.129750   0.021800 15.863000  -5.952  2.1e-05 ***
structurenometa        -0.005649   0.021795 15.907000  -0.259    0.799
sspoly:structurenometa  0.041749   0.030827 15.885000   1.354    0.195
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -309.0   -293.7    159.5   -319.0      151
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.75074 -0.67755 -0.01203  0.72468  2.15529
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000308 0.01755
 Residual             0.007315 0.08553
Number of obs: 156, groups:  line, 16
Fixed effects:
                Estimate Std. Error       df t value Pr(>|t|)
(Intercept)      2.21577    0.01400 15.53400 158.217  < 2e-16 ***
sspoly          -0.10900    0.01627 15.90600  -6.697 5.28e-06 ***
structurenometa  0.01535    0.01627 15.90600   0.943     0.36
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Generation 47

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure +(1|line)
     AIC      BIC   logLik deviance df.resid
  -369.2   -351.0    190.6   -381.2      148
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.7546 -0.5569 -0.0106  0.6894  2.4407
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.001085 0.03294
 Residual             0.004337 0.06586
Number of obs: 154, groups:  line, 16
Fixed effects:
                       Estimate Std. Error       df t value Pr(>|t|)
(Intercept)             2.13797    0.01956 15.83200 109.306   <2e-16 ***
sspoly                 -0.01227    0.02772 15.95400  -0.443   0.6638
structurenometa        -0.05706    0.02778 16.09300  -2.054   0.0566 .
sspoly:structurenometa  0.06523    0.03920 15.96400   1.664   0.1157
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -368.6   -353.5    189.3   -378.6      149
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.8359 -0.5039  0.0152  0.6104  2.3577
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.001343 0.03665
 Residual             0.004340 0.06587
Number of obs: 154, groups:  line, 16
Fixed effects:
                Estimate Std. Error       df t value Pr(>|t|)
```


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```
(Intercept)      2.12169    0.01832 15.73200 115.782   <2e-16 ***
sspoly           0.02033    0.02119 15.80800   0.960    0.352
structurenometa -0.02435    0.02119 15.80700  -1.149    0.268
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Evolution of sexual size dimorphism (across generations)

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure + ss:sex
+ structure:sex + gen + ss:structure:sex + sex + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -3043.3  -2981.1   1533.6  -3067.3     1302
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.5800 -0.6589 -0.0043  0.6784  3.0072
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0001499 0.01224
 Residual             0.0055925 0.07478
Number of obs: 1314, groups:  line, 16
Fixed effects:
                              Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                   2.034e+00  9.210e-03  3.850e+01 220.889  < 2e-16 ***
sspoly                       -2.846e-02  1.199e-02  2.770e+01  -2.373  0.02482 *
structurenometa              -3.959e-03  1.197e-02  2.760e+01  -0.331  0.74342
gen18                         4.358e-03  5.103e-03  1.298e+03   0.854  0.39320
gen32                         1.396e-01  5.964e-03  1.298e+03  23.410  < 2e-16 ***
sexmale                      -1.442e-01  8.197e-03  1.298e+03 -17.586  < 2e-16 ***
sspoly:structurenometa        2.517e-02  1.696e-02  2.770e+01   1.484  0.14900
sspoly:sexmale                3.559e-02  1.168e-02  1.298e+03   3.047  0.00236 **
structurenometa:sexmale      -1.182e-02  1.163e-02  1.298e+03  -1.016  0.30963
sspoly:structurenometa:sexmale -3.671e-03  1.651e-02  1.298e+03  -0.222  0.82407
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss +structure +ss:sex +gen+sex+(1|line)
     AIC      BIC   logLik deviance df.resid
 -3044.2  -2997.5   1531.1  -3062.2     1305
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.6516 -0.6559  0.0026  0.6709  3.0590
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0001843 0.01358
 Residual             0.0056043 0.07486
Number of obs: 1314, groups:  line, 16
Fixed effects:
                  Estimate Std. Error         df t value Pr(>|t|)
(Intercept)      2.031e+00  8.329e-03  3.410e+01 243.906  < 2e-16 ***
sspoly          -1.580e-02  8.977e-03  2.590e+01  -1.761   0.0901 .
structurenometa  1.701e-03  7.946e-03  1.590e+01   0.214   0.8332
gen18            4.412e-03  5.108e-03  1.298e+03   0.864   0.3879
gen32            1.397e-01  5.971e-03  1.298e+03  23.396  < 2e-16 ***
sexmale         -1.500e-01  5.820e-03  1.298e+03 -25.778  < 2e-16 ***
sspoly:sexmale   3.365e-02  8.262e-03  1.298e+03   4.073 4.92e-05 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Evolution of sexual size dimorphism (per generations)

Generation 13

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Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure + ss:sex
+ structure:sex + ss:structure:sex + sex + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -823.9   -786.5    422.0   -843.9      303
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.78833 -0.61194 -0.02139  0.72854  2.27614
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000201 0.01418
 Residual             0.003809 0.06172
Number of obs: 313, groups:  line, 16
Fixed effects:
                                Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                      2.03600    0.01206  33.83000 168.806   <2e-16 ***
sspoly                           0.01950    0.01706  33.83000   1.143   0.2610
structurenometa                 -0.03809    0.01713  34.37000  -2.223   0.0329 *
sexmale                         -0.14725    0.01380 296.83000 -10.670   <2e-16 ***
sspoly:structurenometa           0.02332    0.02422  34.37000   0.962   0.3425
sspoly:sexmale                  -0.00339    0.01971 296.91000  -0.172   0.8636
structurenometa:sexmale          0.00521    0.01958 296.90000   0.266   0.7903
sspoly:structurenometa:sexmale  -0.01274    0.02792 296.94000  -0.456   0.6486
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + sex + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -830.5   -808.1    421.3   -842.5      307
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.76867 -0.63929 -0.03174  0.74251  2.36390
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0002186 0.01479
 Residual             0.0038178 0.06179
Number of obs: 313, groups:  line, 16
Fixed effects:
                  Estimate Std. Error         df t value Pr(>|t|)
(Intercept)       2.032906   0.009443  20.900000 215.272   <2e-16 ***
sspoly            0.026276   0.010173  15.850000   2.583   0.0201 *
structurenometa  -0.027037   0.010172  15.840000  -2.658   0.0173 *
sexmale          -0.149438   0.006987 296.960000 -21.387   <2e-16 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Generation 18

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure + ss:sex
+ structure:sex + ss:structure:sex + sex + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -1641.5  -1596.2    830.7  -1661.5      675
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.8148 -0.6550  0.0063  0.6332  3.1279
Random effects:
 Groups   Name        Variance Std.Dev.
```


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```
 line     (Intercept) 0.000194 0.01393
 Residual             0.005062 0.07114
Number of obs: 685, groups:  line, 16
Fixed effects:
                               Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                    2.013500   0.010395  30.500000 193.692   <2e-16 ***
sspoly                        -0.004289   0.014777  31.200000  -0.290    0.774
structurenometa                0.014164   0.014702  30.500000   0.963    0.343
sexmale                       -0.115432   0.010820 669.100000 -10.668   <2e-16 ***
sspoly:structurenometa         0.018326   0.020862  30.900000   0.878    0.386
sspoly:sexmale                 0.011375   0.015417 669.200000   0.738    0.461
structurenometa:sexmale       -0.017930   0.015325 669.200000  -1.170    0.242
sspoly:structurenometa:sexmale -0.011589   0.021755 669.200000  -0.533    0.594
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + structure:sex + sex +
(1 | line)
     AIC      BIC   logLik deviance df.resid
 -1646.5  -1614.8    830.2  -1660.5      678
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.8278 -0.6721  0.0119  0.6464  3.1030
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000204 0.01428
 Residual             0.005065 0.07117
Number of obs: 685, groups:  line, 16
Fixed effects:
                         Estimate Std. Error         df t value Pr(>|t|)
(Intercept)              2.007565   0.008702  25.100000 230.708   <2e-16 ***
sspoly                   0.007734   0.008977  16.000000   0.862   0.4017
structurenometa          0.023243   0.010551  30.400000   2.203   0.0353 *
sexmale                 -0.109841   0.007711 669.200000 -14.245   <2e-16 ***
structurenometa:sexmale -0.023615   0.010881 669.200000  -2.170   0.0303 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Generation 32

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:structure + ss:sex
+ structure:sex + ss:structure:sex + sex + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -688.2   -650.7    354.1   -708.2      306
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.1659 -0.6642  0.0271  0.7107  2.2938
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0005957 0.02441
 Residual             0.0058892 0.07674
Number of obs: 316, groups:  line, 16
Fixed effects:
                               Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                    2.226013   0.017209  27.630000 129.350  < 2e-16 ***
sspoly                        -0.130612   0.024505  28.350000  -5.330 1.08e-05 ***
structurenometa               -0.004916   0.024499  28.340000  -0.201    0.842
sexmale                       -0.202288   0.017160 299.820000 -11.788  < 2e-16 ***
```


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```
sspoly:structurenometa           0.041878   0.034651  28.340000   1.209    0.237
sspoly:sexmale                   0.129661   0.024436 300.050000   5.306 2.18e-07 ***
structurenometa:sexmale         -0.020159   0.024430 299.890000  -0.825    0.410
sspoly:structurenometa:sexmale   0.021086   0.034553 299.970000   0.610    0.542
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: elytrum ~ ss + structure + ss:sex + sex +(1|line)
     AIC      BIC   logLik deviance df.resid
  -690.7   -664.4    352.4   -704.7      309
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.2339 -0.6714  0.0426  0.7232  2.3257
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0007672 0.02770
 Residual             0.0059028 0.07683
Number of obs: 316, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)       2.21796    0.01540  22.31000 143.982  < 2e-16 ***
sspoly           -0.10963    0.01853  26.20000  -5.917 2.96e-06 ***
structurenometa   0.01119    0.01633  15.86000   0.686    0.503
sexmale          -0.21237    0.01223 299.94000 -17.368  < 2e-16 ***
sspoly:sexmale    0.14016    0.01730 299.99000   8.104 1.35e-14 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Evolution of male and female body weight at generation 45 (analysis including EL as covariate)

Males

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + ss:structure + centelytrum
+ (1 | line)
     AIC      BIC   logLik deviance df.resid
 -4170.6  -4144.4   2092.3  -4184.6      305
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.8949 -0.6317 -0.0604  0.5979  4.5689
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 1.527e-08 0.0001236
 Residual             8.097e-08 0.0002845
Number of obs: 312, groups:  line, 16
Fixed effects:
                         Estimate Std. Error         df t value Pr(>|t|)
(Intercept)             5.111e-03  6.978e-05  1.590e+01  73.240  < 2e-16 ***
sspoly                  3.288e-04  9.848e-05  1.580e+01   3.339  0.00423 **
structurenometa         1.226e-04  9.848e-05  1.580e+01   1.245  0.23140
centelytrum             5.200e-03  2.577e-04  4.028e+02  20.177  < 2e-16 ***
sspoly:structurenometa -1.523e-04  1.404e-04  1.630e+01  -1.084  0.29413
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + centelytrum + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -4171.5  -4149.0   2091.7  -4183.5      306
```


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```
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.8698 -0.6223 -0.0591  0.5856  4.5745
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 1.671e-08 0.0001293
 Residual             8.096e-08 0.0002845
Number of obs: 312, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)     5.148e-03  6.305e-05 1.630e+01  81.641  < 2e-16 ***
sspoly          2.538e-04  7.267e-05 1.620e+01   3.492  0.00296 **
structurenometa 4.764e-05  7.269e-05 1.620e+01   0.655  0.52138
centelytrum     5.167e-03  2.566e-04 3.963e+02  20.136  < 2e-16 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Females

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + ss:structure + centelytrum
+ (1 | line)
     AIC      BIC   logLik deviance df.resid
 -3880.3  -3854.2   1947.2  -3894.3      300
Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.4669 -0.6164 -0.0469  0.6068  3.0758
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 4.844e-09 0.0000696
 Residual             1.774e-07 0.0004212
Number of obs: 307, groups:  line, 16
Fixed effects:
                        Estimate Std. Error         df t value Pr(>|t|)
(Intercept)             7.207e-03  5.954e-05  1.580e+01 121.054  < 2e-16 ***
sspoly                  2.484e-04  8.438e-05  1.600e+01   2.944  0.00953 **
structurenometa         2.105e-04  8.315e-05  1.511e+01   2.532  0.02292 *
centelytrum             6.209e-03  3.632e-04  2.653e+02  17.097  < 2e-16 ***
sspoly:structurenometa -2.344e-04  1.210e-04  1.668e+01  -1.938  0.06974 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + centelytrum + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -3879.0  -3856.6   1945.5  -3891.0      301
Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.4282 -0.6121 -0.0463  0.5739  2.9443
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 8.249e-09 9.082e-05
 Residual             1.773e-07 4.211e-04
Number of obs: 307, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)     7.260e-03  5.866e-05 1.718e+01 123.773   <2e-16 ***
sspoly          1.364e-04  6.815e-05 1.764e+01   2.001    0.061 .
structurenometa 9.920e-05  6.702e-05 1.659e+01   1.480    0.158
centelytrum     6.091e-03  3.635e-04 2.691e+02  16.755   <2e-16 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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Model: Evolution of male and female body weight at generation 45 (analysis without EL as covariate)

Males

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + ss:structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -3908.1  -3885.6   1960.0  -3920.1      308
Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.7512 -0.6678 -0.0591  0.5372  2.8880
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 5.061e-08 0.000225
 Residual             2.025e-07 0.000450
Number of obs: 314, groups:  line, 16
Fixed effects:
                       Estimate Std. Error        df t value Pr(>|t|)
(Intercept)            5.037e-03  1.235e-04 1.602e+01  40.785   <2e-16 ***
sspoly                 3.164e-04  1.745e-04 1.599e+01   1.813   0.0887 .
structurenometa        1.133e-04  1.745e-04 1.599e+01   0.649   0.5254
sspoly:structurenometa 1.862e-04  2.468e-04 1.599e+01   0.754   0.4615
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -3909.5  -3890.8   1959.8  -3919.5      309
Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.7373 -0.6693 -0.0711  0.5204  2.8752
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 5.277e-08 0.0002297
 Residual             2.025e-07 0.0004500
Number of obs: 314, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)     4.990e-03  1.088e-04 1.600e+01  45.863  < 2e-16 ***
sspoly          4.095e-04  1.256e-04 1.598e+01   3.260  0.00492 **
structurenometa 2.064e-04  1.256e-04 1.598e+01   1.644  0.11978
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Females

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + ss:structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -3706.9  -3684.5   1859.5  -3718.9      305
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.76283 -0.66887 -0.05672  0.66834  2.99231
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 5.300e-08 0.0002302
 Residual             3.496e-07 0.0005913
Number of obs: 311, groups:  line, 16
```


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```
Fixed effects:
                        Estimate Std. Error        df t value Pr(>|t|)
(Intercept)            7.076e-03  1.332e-04 1.606e+01  53.134   <2e-16 ***
sspoly                 3.323e-04  1.887e-04 1.617e+01   1.761   0.0971 .
structurenometa        2.014e-04  1.880e-04 1.596e+01   1.071   0.3001
sspoly:structurenometa 1.543e-04  2.665e-04 1.609e+01   0.579   0.5705
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -3708.6  -3689.9   1859.3  -3718.6      306
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.77446 -0.66486 -0.07425  0.66432  2.97477
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 5.449e-08 0.0002334
 Residual             3.496e-07 0.0005913
Number of obs: 311, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)     7.038e-03  1.166e-04 1.607e+01  60.381  < 2e-16 ***
sspoly          4.097e-04  1.346e-04 1.609e+01   3.043  0.00771 **
structurenometa 2.782e-04  1.346e-04 1.609e+01   2.067  0.05524 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Evolution of male and female body weight at generation 46

Males

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + ss:structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -1951.5  -1933.0    981.7  -1963.5      154
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.52354 -0.66796 -0.05558  0.74111  2.65187
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 6.509e-08 0.0002551
 Residual             2.405e-07 0.0004904
Number of obs: 160, groups:  line, 16
Fixed effects:
                         Estimate Std. Error         df t value Pr(>|t|)
(Intercept)             0.0055275  0.0001493 15.9870000  37.027   <2e-16 ***
sspoly                  0.0001200  0.0002111 15.9870000   0.568    0.578
structurenometa        -0.0000450  0.0002111 15.9870000  -0.213    0.834
sspoly:structurenometa  0.0003800  0.0002986 15.9870000   1.273    0.221
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -1951.9  -1936.5    981.0  -1961.9      155
```


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```
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.5565 -0.7137 -0.1020  0.7024  2.6805
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 7.412e-08 0.0002722
 Residual             2.405e-07 0.0004904
Number of obs: 160, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)     5.432e-03  1.357e-04 1.599e+01  40.042   <2e-16 ***
sspoly          3.100e-04  1.567e-04 1.599e+01   1.979   0.0653 .
structurenometa 1.450e-04  1.567e-04 1.599e+01   0.926   0.3684
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Females

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + ss:structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -1878.1  -1859.7    945.0  -1890.1      153
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.39616 -0.60645  0.04018  0.53339  2.59546
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 1.282e-07 0.0003581
 Residual             3.446e-07 0.0005870
Number of obs: 159, groups:  line, 16
Fixed effects:
                       Estimate Std. Error        df t value Pr(>|t|)
(Intercept)            7.448e-03  2.017e-04 1.594e+01  36.928   <2e-16 ***
sspoly                 8.941e-05  2.856e-04 1.603e+01   0.313    0.758
structurenometa        1.325e-04  2.852e-04 1.594e+01   0.465    0.649
sspoly:structurenometa 3.131e-04  4.037e-04 1.599e+01   0.776    0.449
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: bw ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
 -1879.5  -1864.2    944.7  -1889.5      154
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.42046 -0.62878  0.00425  0.52945  2.55961
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 1.345e-07 0.0003667
 Residual             3.446e-07 0.0005870
Number of obs: 159, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)     7.369e-03  1.780e-04 1.597e+01  41.399   <2e-16 ***
sspoly          2.462e-04  2.056e-04 1.600e+01   1.197    0.249
structurenometa 2.888e-04  2.056e-04 1.600e+01   1.404    0.179
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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Chapter 3

Experimental evolution of population subdivision and sexual selection fails to induce responses in female mating rates but suggest that the effects of sexual conflict are reversed in spatially structured populations

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Experimental evolution of population subdivision and sexual selection fails to induce responses in female mating rates but suggest that the effects of sexual conflict are reversed in spatially structured populations.

Eduardo Rodriguez-Exposito [1] and Francisco Garcia-Gonzalez [1,2]

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Abstract

The origin and evolutionary maintenance of polyandrous behaviour is a conundrum. A recent theoretical study has suggested that a polyandrous strategy would be favoured in subdivided populations because in these situations female multiple mating can effectively work as a risk-spreading bet-hedging strategy protecting polyandrous females against complete reproductive failure. In this study we carry out an empirical test of some of these ideas using experimental evolution. We have assessed mating rates, the propensity to remate, remating intervals and longevity of female seed beetles (*Callosobruchus maculatus*) that evolved for 12 and 30 generations under four different selection regimes generated by a 2x2 factorial design resulting from the combination of mating system (monogamy / polygamy) and population spatial structure (structured / unstructured) selection treatments. In addition, due to the relevance of the rates of infertile males in determining the likelihood of bet-hedging benefits associated to polyandrous behaviour, we assessed infertile mating rates in our four selection regimes. Our results suggested that neither the mating system, nor the population spatial structure or their interaction had an effect on female mating rates, the propensity to remate or the remating interval, probably because there were no differences in regards to the male infertility rates among the selection regimes, which were consistently low in this model system and under the experimental conditions imposed. However, our analysis brought to light a remarkable interaction between the two selection treatments on female longevity. The patterns in female longevity (when females mated to standardized tester males from outside the selection experiment) found in non-structured populations supported the predictions derived from sexual conflict theory, with polyandrous females living longer than their monogamous counterparts (as expected if females evolve resistance traits to the presence of male adaptations that depress female fitness), but interestingly the pattern was reversed in subdivided populations: females from monogamous selection lines lived for longer than females that evolved under the presence of sexual selection. This intriguing result, which was consistent across generations, warrant future research into the mechanisms involved. Our study clearly indicates that spatial population structure moderates sexual selection and sexual conflict in unexpected ways.

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Introduction

The evolution of polyandry (female multiple mating with different males) is a controversial question in the study of the evolution of mating systems (Jennions and Petrie 2000; Garcia-Gonzalez and Simmons 2005; Pizzari and Wedell 2013; Yasui and Garcia-Gonzalez 2016). Mating entails well-known costs, from simple energetic costs to increases in the risk of predation or the risk of contracting sexually transmitted diseases (Daly 1978; Chapman et al. 1995; Blanckenhorn et al. 2002). Nevertheless, the cost of mating differs between males and females due to the differential investment in reproduction they make in relation to gamete production and parental care for instance (Parker et al. 1972; Trivers 1972; but see Kokko and Jennions 2008). In general, in those species with anisogamy (Bateman 1948), males are the sex which produces smaller gametes which entail very little costs in term of metabolic energy, whereas females invest considerable energy to generate every sex cell (ovum). Thus, male's reproductive success is not limited his ability by to produce sex cells but his ability to fertilize female eggs, whereas on the contrary female's reproductive success is indeed limited by her ability to produce sex cells. In addition to that, in many species there is a lapse of time after copulation in which one or both parents take care of their offspring (post-mating parental care). The contribution of each sex on this task varies among taxa (Kokko and Jennions 2008). More precisely, among invertebrate species with parental care, female-only care is the most common option (Zeh and Smith 1985; Tallamy 2000). Those differences are among the causes that root the definition of the traditional sex roles in which males are the sex which compete more intensely to get access to females and females choose among the potential available mates in order to obtain benefits for the offspring they will take care of (Kokko and Jennions 2008; Fritzsche and Arnqvist 2013). Consequently, each sex follows different strategies to optimize its fitness. From the male perspective, multiple mating has a clear adaptive meaning easy to understand, the higher the number of mates, the higher the probability to sire a greater amount of offspring maximizing in that sense their fitness. On the contrary, due to the limited number of high-cost ova and the multiple additional costs derived from reproduction, females tend to be more choosy at mate choice and consequently, their strategy to optimize their fitness is based on the selection of a good quality mate instead of increasing the number of matings (Bateman 1948; Andersson 1994). Furthermore, females generally receive enough sperm in a single copulation event to fertilize all their ova, so remating might seem to be, at least at first glance, unnecessary from the point of view of ensuring fertilization (Eady 1995 and references therein; Wilson and Tomkins 2014).

Despite the known costs of mating and polyandrous behavior, female multiple mating is widespread in nature (Ridley 1990; Jennions and Petrie 2000; Simmons 2001b; Zeh and Zeh 2001; Pizzari and Wedell 2013; Taylor et al. 2014). Thus, the origin and maintenance of polyandrous behavior remains a conundrum from an evolutionary point of view and two main groups of hypotheses have been proposed as a potential explanation. On the one hand, it has been suggested that polyandry could be a side effect resulting from sexual conflict and antagonistic sexual selection based on the different evolutionary interests between sexes over copulation and mating rates. So, polyandry could be considered the result of a non-adaptive correlated response to selection on males to elevate mating rates,

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which are in turn suboptimal mating levels for females (Halliday and Arnold 1987). On the other hand, a second group of hypotheses suggests that polyandry can be explained from an adaptive point of view due to the benefits that females obtain by mating with different males. Benefits accrued by females could be direct (also known as material), for example, when males transfer nuptial gifts or when further matings are needed to ensure fertilization of the complete set of ova (Arnqvist and Nilsson 2000; Simmons 2001b). In many species, however, direct benefits are unable to explain female mating frequencies and this prompted the suggestion that females might also obtain indirect (genetic) benefits from mating with several males. Indeed, research over the last decades has provided ample theoretical and experimental evidence for the existence of genetic benefits associated to polyandrous behaviour (Yasui 1998; Newcomer et al. 1999; Evans and Magurran 2000; Jennions and Petrie 2000; Garcia-Gonzalez and Simmons 2005; Simmons 2005; Fisher et al. 2006; Garcia-Gonzalez and Simmons 2007; Garcia-Gonzalez et al. 2015 and see meta-analysis by Slatyer et al. 2012). For instance, polyandry is thought to allow females to obtain good genes or compatible genes that may enhance the viability, the survival or the reproductive success of their offspring (Jennions and Petrie 2000; Zeh and Zeh 2003; Garcia-Gonzalez and Simmons 2005; Neff and Pitcher 2005; Simmons 2005; Garcia-Gonzalez and Simmons 2007, 2011).

The hypotheses on benefits of female multiple mating above are based on the existence of female mate choice, either precopulatory or postcopulatory (cryptic female choice). Nonetheless, female mate choice can be unreliable if it is based on uncertain information about male quality (Castellano 2009), or if environmental conditions change continuously and female discrimination of best or most suitable mate genotypes is not useful given the uncertainty surrounding the future environmental conditions that the offspring will experience.. In these situations, multiple mating could function as a bet-hedging, risk spreading, strategy of the kind 'don't put all your eggs in one basket' (Philippi and Seger 1989; Yasui 1998; Hopper 1999; Fox and Rauter 2003; Starrfelt and Kokko 2012; Garcia-Gonzalez et al. 2015; Holman 2016; Yasui and Garcia-Gonzalez 2016; Yasui and Yoshimura 2018). According to the bet-hedging hypothesis for the evolution of polyandry females that mate multiply would increase the probabilities that at least part of their offspring are sired by a suitable mate, simply because they sample more males. In that sense, under the light of bet-hedging, polyandrous behavior would minimize the consequences of any possible assessment error in mate choice, and in fact, the strategy does not require any sire selection criteria to be successful (Yasui 1998; Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016). This is specially the case in situations where the frequency of unsuitable males in the population is high, as it is seems to be the case in many natural populations regarding, for instance, male infertility problems (Garcia-Gonzalez 2004; Greenway et al. 2015; Greenway and Shuker 2015; Yasui and Garcia-Gonzalez 2016; Yasui and Yoshimura 2018).

Populations are frequently subdivided into different subunits that are more or less interconnected by migration. In this situations, the number of possible mates could be limited (Levin 1974; Hanski 1999), leading to higher rates of inbreeding,

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reproductive isolation and extinction (Saccheri et al. 1998; Haikola et al. 2001). In a recent theoretical paper, Yasui and Garcia-Gonzalez (2016) carried out computer simulations to shed light on whether bet-hedging can be a key mechanism favouring the maintenance of polyandrous behavior in spatially structured populations. The results of this study underscored the potential of bet-hedging to provide benefits to polyandrous females over monandrous females in evolutionary terms, primarily in small populations or in large populations that are subdivided into smaller demes. In other words, Yasui and Garcia-Gonzalez (2016) results suggest that a bet-hedging mechanism may underlie the evolutionary maintenance of polyandry in populations that are not panmictic. Yasui and Garcia-Gonzalez (2016) study constitutes a rare investigation into the connection between mating system evolution (or sexual selection in general, for that matter) and metapopulation structuring. In fact, the lack of knowledge on this presumably important connection is surprising given that the study of metapopulation structure has received increasing attention during the last five decades and it is now clear that such spatial structuring of populations has important ecological and evolutionary ramifications (Levins 1969; Hanski and Gilpin 1991; Hanski 1999; Hanski et al. 2011). Despite this profusion of research, we know very little about the implications of population subdivision on sexual selection including, mating rates. Other than Yasui and Garcia-Gonzalez (2016) we are not aware of any explicit study on these questions, and notably, empirical research is absent. In this chapter we aim to fill this important gap in knowledge.

Here, we use *Callosobruchus maculatus*, a tractable model system (see Chapter 1), and exploit the power of experimental evolution (Garland and Rose 2009; Garcia-Gonzalez 2011; Kawecki et al. 2012) to study, for the first time, the effect of selection associated to metapopulation structure on the evolution of female mating rates, a key trait that largely determines the mating system of a population, and the opportunity and strength of sexual selection. As our approach was designed to investigate empirically the consequences of population spatial structure on the evolutionary divergence in female mating frequency, the results can be placed in the context of testing some of the ideas put forward by Yasui and Garcia-Gonzalez (2016) on the evolution of polyandry in subdivided populations. In addition to the manipulation of population subdivision our approach also imposed variation in mating system by removing sexual selection (through enforced monogamy) in half of our experimental populations. In this way, our protocol can answer whether the interaction between the presence or absence of sexual selection, and population structure, moderates female propensity to remate. We also focused in our study on another key female trait, female longevity. This life-history trait is relevant in the context of mating frequency given that our chosen study model is characterized by intense sexual conflict crystalized by male harassment and mating interactions that is thought to impact on female lifespan. Finally, our study took into account the presence of infertile males in the population, a feature with a paramount relevance in determining the outcome of reproductive and population dynamics (Garcia-Gonzalez 2004). Since the frequency of infertile males in a population is predicted to be a key factor determining the scope for females to obtain bet-hedging based benefits from multiple mating (Yasui and Garcia-Gonzalez 2016), we decided to explore the variation in infertile mating rates among the different selection lines because this population feature, which can be directly linked to

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potential variation in female mating frequency, may help us to clarify potential differences among our selection regimes.

Material and methods

In this study we investigate divergence in mating rates and longevity of females from the selection lines when given multiple opportunities for mating/remating. In addition, we assayed the divergence in infertile mating rates among the different lines. Focal individuals were sourced from four different selection regimes that we imposed in a 2x2 factorial design combining mating system selection history (monandry/polyandry) and spatial population structure selection history (metapopulation structure/absence of population spatial structure). Details about the selection experiment has been described in detail in Chapter 1 (The Experimental Evolution Approach section). Basic information regarding the biology of our study model (Study Animals section) and the source population (Stock Population section) has also been provided in Chapter 1.

Traits

Five main response variables were measured in focal females (i.e., females coming from the selection lines) that were given a fixed number of opportunities to mate with tester individuals (see below): (i) total number of matings across all mating opportunities, (ii) remating proportion, the number of times each female remated out of the number of remating opportunities, (iii) remating interval (the number of days between a female's first and second mating), (iv) female longevity (after being exposed to the mating opportunities and after mating; all females mated at least once and no female died before the end of the mating opportunities period). We also measured on a different set of individuals (focal males and focal females) (v) rates of infertile matings, by noting down whether individual focal females generated adult offspring after a single copulation with a focal male.

Female mating rates

Two replicates of the experiments for assessing divergence in female mating frequency and longevity were run, after 12 and 30 generations of evolution under the different selection regiments. The reproductive behaviour of a total of 272 virgin focal females (generation 12: 7 females per each of the 16 replicatesd lines (n = 112); generation 30: 10 females per replicate line (n = 160)) was analyzed. All focal females were 1 to 3 days old when the experimental replicates were carried out (mean ± SE = 1.49 ± 0.002). Each focal female was allowed to mate with a single standardized tester male (a different male for each mating opportunity) for 15 minutes once daily for 12 days (generation 12), or 10 days (generation 30). All mating opportunities within each experimental replicate were given in the mornings, to avoid noise due to a potential influence of circadian rhythm on the propensity of mating. Each mating opportunity was videotaped. Mating opportunities were carried out in 1 x 1 x 5 cm glass vials. After 15 min the male was removed and the female was transferred to a 1.5 ml Eppendorf tube until the next mating opportunity 24 h later. Glass vials were washed with soap and water

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between mating opportunities to avoid possible effects of residuals pheromones from individuals previously placed in those vials. Females did not have access to oviposition substrate during or between subsequent mating opportunities. A few females laid eggs on the walls of the Eppendorf tubes where they were resting between mating opportunities.

We minimized variation attributable to mate identity in the estimation of female mating rates by using standardized males. This is important as female refractoriness, and therefore female mating rates, are known to be highly dependent on substances transferred in the ejaculate during copulation in a range of species (e.g. Cordero 1995; Wolfner 1997; Wolfner 2002; Gillott 2003; Bailey and Nuhardiyati 2005; Himuro and Fujisaki 2008; Yamane et al. 2008; Yamane and Miyatake 2010c, b; Yamane et al. 2015). This implies that intrinsic (i.e., genetic) and environmental male effects, as well as potential male x female effects are likely to introduce variance in estimations of female remating rates, unless male identity is standardized (Travers et al. 2015; Travers et al. 2016 and see rationale in Garcia-Gonzalez and Evans 2011).

We generated standardized tester males by culturing inbred, near-isogenic lines. The methodology to generate these lines has been described in detail in Chapter 1 (The Experimental Evolution Approach section). We used tester males that belonged to a same near-isogenic line in each mating opportunity. That is, all females across all selection lines were exposed to the same ID tester males each mating opportunity, and the ID of the near-isogenic line used to generate the tester males were rotated across mating opportunities. By using a wide range of male tester genotypes we aimed to minimize as much as possible variation attributable to male by female interactions affecting female mating behaviour (e.g., due to male by female effects on female responses in refractoriness after the receipt of ejaculate during mating) (e.g see Travers et al. 2015; Travers et al. 2016). Tester males used in this experiment were collected from near-isogenic lines that had been cultured for 15 and 33 generations, for the experimental replicates at generations 12 and 30, respectively. The range of ages among tester males used in each mating opportunity (i.e., within each near-isogenic line) never exceeded 6 days, and in any case across all tester males no older than 7 days-old males were used, and variation in age was spread among the tested focal individuals. The 1.5 ml Eppendorf tubes where the females rested after each mating opportunity were monitored once daily for survival to record female longevity. Figure 3.1a provides an outline of the experiment and assays.

Infertile matings

Given that male infertility is a key factor in determining the potential for bet-hedging based benefits of polyandry to take place (Yasui and Garcia-Gonzalez 2016), we tested if there were differences in the rates of infertile matings due to male effects among the four different selection regimes. This test was carried out at generation 34 of the experimental evolution protocol. We randomly selected 10 focal males per line (n= 160) and mated each with a randomly selected female from the same selection line as the male in a 1 x 1 x 5 cm glass vial. We allowed them 20 minutes to mate. Glass vials were visually inspected and copulations were confirmed in all cases. Afterwards, the female was placed in a small plastic

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container (30 ml) with mung beans *ad libitum* for egg laying and removed from these oviposition vials 48 hours later. While the assays above inform on rates of infertile matings they are not informative on the extent to which these may be due to exclusive male effects. To get a more accurate picture of the extent of male infertility in the replicated populations we also mated another set of focal males (n= 160) with tester females (10 males per line, each male mated with a female as before) and the same experimental protocol described above was followed. In both cases the oviposition vials were checked 29 days after the moment in which the females were removed from them, to confirm for the presence or absence of offspring. Due to development times under our laboratory conditions (see Chapter 1), and taking into account that females lay most of their eggs soon after the last copulation, and typically within the following few days (e.g., 90% of the lifetime offspring production by females is attributable to oviposition within the first three days after mating; Zajitschek et al. 2018 in press, and see also Credland and Wright 1989 and Chapter 4), a period of 29 days is long enough to ensure that most, if not all, the offspring complete development and emerge as adults from the beans when the vials were checked. We also noted down whether they produced less or more than 10 offspring, a threshold set arbitrarily, but which can be used as an additional indication of infertility related problems leading to a decline in female productivity (females typically lay several dozens of eggs in the next two days following a mating; see Chapter 4). For instance, sperm limited males or males with physiological problems or mechanical infertility (Garcia-Gonzalez 2004) may not be completely infertile but can lead to low fecundity of their mates, which may presumably have similar consequences for variation in female mating behaviour than completely infertile matings. The age of the individuals at mating ranged between 1-2 days (mean ± SE = 1.97 ± 0.001 (n = 318)) old for males and among 1-5 days old for females (mean ± SE = 3.20 ± 0.004 (n = 318)). The age of males and females when the mating events were carried out, as well as the female type (tester or focal) were included in the models to control the results for those factors. The response for the analysis of the infertile mating rates was encoded as '1' whether the female produced adult offspring (or whether they reach our fertility threshold in our second analysis) or '0' otherwise.

Tester females used in this experiment were extracted from Standardized Heterozygous Lines (SHL) that were 6 generations-old (undergoing population growth to generate enough tester individuals) and that were created crossing near-isogenic lines that had underwent 32 generations of inbreeding following brother-sister matings (see Chapter 1, section Tester individuals from near-isogenic lines for details, for more details). All the tester individuals belonged to the same SHL so that we had a standardized homogeneous genetic background with which to test divergence among selection regimes. Figure 3.1b provides an outline of the experiment.

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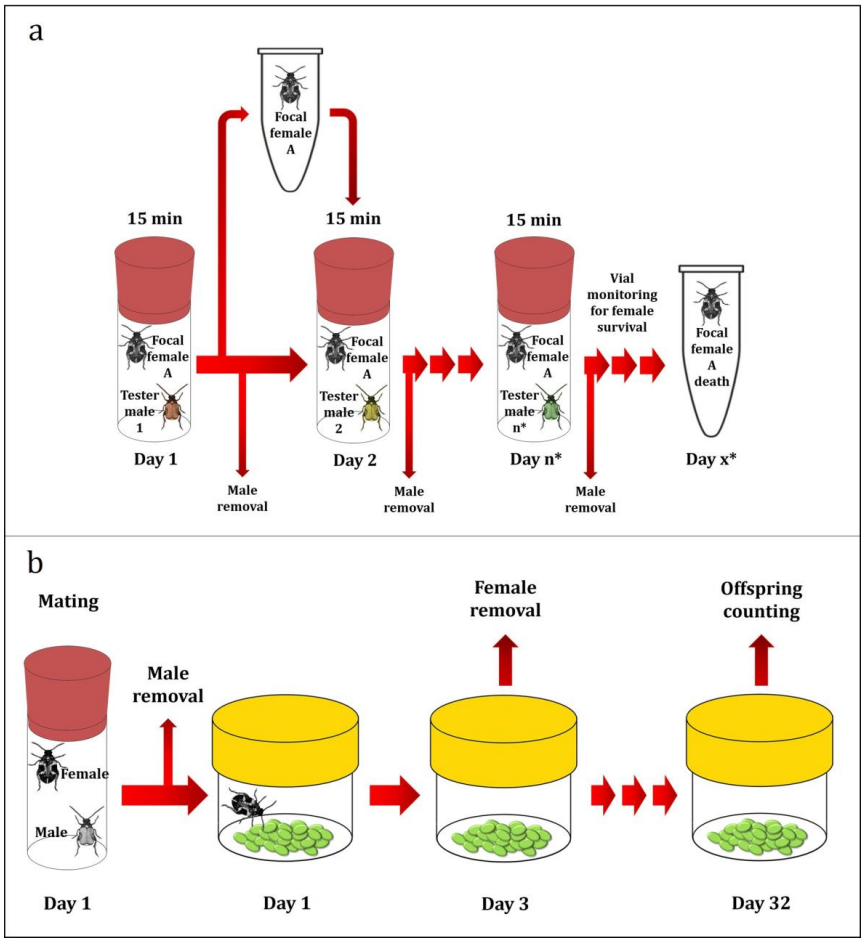

Fig. 3.1. Experimental protocols to assess variation in female mating rates and female longevity (a), and the rates of infertile matings (b).

(a) To assess female mating rates and female longevity each female was placed daily (12 days for females from generation 12, 10 days for females from generation 33) with a standardized tester male in a glass vial for 15 minutes. At the end of that period the tester male was removed and the female was isolated in a 1.5 Eppendorf tube until the next mating opportunity (24 hours later). Tester males were extracted from a different inbred line each mating opportunity. After all the mating opportunities were completed females remained in their isolation vials, which were checked once daily until female death.

(b) To assess the rate of infertile matings a focal male and a female from the same selection line (n = 160 (10 pairs per selection line)) were placed together in a crystal vial for 20 minutes, time enough for a single copulation to occur. After that time, the male was

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removed and the female was transferred to a small plastic container with beans for 48 hours to allow the egg laying process. On day 3, the female was removed from the oviposition vial. Twenty-nine days later (32 since the two breeders were put together) the vials were checked to determine the presence/absence of adult offspring and also whether the females produced more than 10 individuals as complementary information that may be a cue to identify infertility problems. The same protocol was carried out once again using tester females instead of focal males.

Body size

Elytron length (EL) was used as a proxy of body size. Females from the female mating rates assays and both males and females from the infertile mating assays were measured following the protocol described in Chapter 2 (section Material and Methods). All the experimental females used female in the analysis of the female mating rate were measured twice (n = 272 (n = 112 and 160 for generations 12 and 30, respectively) and after that repeatability was calculated following Becker (1984). The measurements of EL were highly repeatable (repeatability > 0.99, $p < 0.0001$). In light of this, mean body size per female was included in the models. Equally, all the individuals from the infertile mating assays were measured twice (n = 320 for either sex). Repeatabilities were calculated once more following Becker (1984) and the measurements of EL were equally highly repeatable regardless for either sex (repeatability > 0.99; $p < 0.0001$ for either sex). Mean body sizes were included as covariates in the models.

Statistical analysis

All the analyses were carried out using R 3.3.2 (R Core Team 2016). Sample size in the analysis of female mating rates was reduced from 272 to 271 females (n = 112 and 159 for generations 12 and 30, respectively) because one female from generation 30 was killed by mistake before the end of the experiment. For the analysis of infertile matings, copulation did not occur in two vials because the males escaped from these vials and so sample size was slightly reduced: the reproductive outcome of 318 females was measured (assay mating focal males to focal females: n = 158 pairs, assay using focal males mated to tester females: n = 160).

Generalized Linear Mixed models (GLMMs) were fitted to the response variables using the functions '*glmer*' implemented within the package '*lme4*' (Bates et al. 2015). For the analysis of the number of matings, the remating proportion and the rate of infertile matings we used a binomial distribution. The R command '*cbind*' was used to taken into account the denominator such that the number of matings was corrected by the number of opportunities given for mating which differed between the two experimental replicates (12 and 10 in generations 12 and 30 respectively). Thus, the response variable contained information of both the number of times females did mate but also the number of times in which females did not. The same protocol was followed for the analysis of the remating proportion but in that case, the response variable included information of the number of times that female remated as nominator and the number of times female did not as denominator. The analysis of the rates of infertile mates was carried out on a binary response variable encoded as "1" whether females produced adult offspring (or they reached the fertility threshold) or "0" whether

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they did not. In the analysis of the remating interval and female longevity the models were rung using a Poisson distribution. The square-root transformation was used in the analysis of remating interval while female longevity remained untransformed. GLMMs for all the variables above, except for the true binomial rates of infertile matings variable, which had dispersion equal to 1, were also run using the function '*glmmPQL*' from the package '*mass*' (Venables and Ripley 2002) to improve the dispersion of the residuals of the models using a quasipoisson or quasibinomial distribution depending on the response variables. The significance of some variables differed between models that were run with *glmmPQL* or with *glmer*; since the models run with *glmer* were overdispersed in the analyses of the number of matings and remating proportion, only the results yielded by *glmmPQL* models are shown.

Remating interval and female longevity can be considered count variables due to the way in which our data were collected. However, both variables measure time and can be considered continuous as well. Furthermore, when a count variable takes a large number of values, as it is the case for female longevity in our experiments, the variable can be treated as continuous (Zuur et al. 2009). For this reason, we run confirmatory LMMs on these two variables using the function '*lmer*' implemented within the package '*lme4*' (Bates et al. 2015). In all cases both LMMs and GLMMs yielded the same results, and thus we show here only the results pertaining to LMMs.

The models included the following variables as predictors: generation, mating system selection treatment (monogamy/polygamy), population spatial structure selection treatment (metapopulation structure/no structure), and the interaction between those two selection treatments, as fixed factors, as well as the replicate line as a random factor nested within each combination of mating system and population spatial structure. In the analysis of the rate of infertile matings generation was not included because this experiment was carried out in a single generation. This analysis, however, included female type (tester/focal) as fixed factor to control for the female origin. The number of covariates included in the models varied depending on the response variable. Female body size was included in all the cases. Additionally, the total number of matings was included as covariate in the models of female longevity. In the case of the rate of infertile matings, not only the female body size was added to the models, but also male body size was included, as well as the age at mating of males and females. All the covariates were mean centered to improve the interpretability of regression coefficients, as recommended by Schielzeth (2010).

We were interested in the contribution of particular effects to variance in the dependent variables (i.e. hypothesis testing) rather than on finding the best model out of many competing ones. Thus, the focus of the analyses was to test the significance of effects. We followed the same protocol in all cases. First, we fitted the full model (the model with all the predictors and their interactions) and tested it against the null model (the model lacking the predictors of interest but including the random structure of the data, i.e., the random factor Selection Line) with a Likelihood Ratio Test (LRT) using the R function '*anova*' with argument test set to '*Chisq*'. It has been suggested that significance tests for individual predictors

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should only be considered once the full model reveals significance, unless an error-level adjustment for multiple testing is used to avoid inflation of Type-I error (Forstmeier and Schielzeth 2011). We adjusted p values for multiple testing using the Benjamini-Hochberg procedure (Benjamini and Hochberg 1995), to correct for such potential source of inflation of Type-I error.

Model reduction was carried out following two different methods depending on the type of models we were fitting to each response variable. For the GLMM models involving a Penalized Quasi-Likelihood estimation (PQL), that is, those on number of matings and remating proportion, we ran progressively simplified models by removing fixed effects (or their interactions), as well as covariates, one-at-a-time when their p-value was non-significant. On the other hand, for the remaining variables we ran progressively simplified models by removing fixed terms one-at-a-time using the '*drop1*' function (argument test set to 'Chi') from the package 'stats' (R Core Team 2016), and testing the effect of removal of each term on the change in model deviance using likelihood ratio tests and maximum likelihood (Bolker et al. 2009). The final model included the significant effects (alpha criterion of 0.05), and we also always retained in the final model the fixed factors mating system and population spatial structure plus the random factor selection line, regardless of the contribution of these factors, to account for the structure of the experimental design and the hierarchical structure of the data (i.e., for the fact that the data is grouped by the random factor within each combination of mating system and population structure selection levels). The LRT for the non-significant effects was calculated using the 'drop1' function after adding the particular non-significant effect to the final model.

While significance of the fixed effects was calculated using maximum likelihood as described above, parameter estimates (coefficients, estimates) of the fixed and random effects in the final model were calculated using Restricted Maximum Likelihood (REML), as it has been suggested (Zuur et al. 2009). The random effect was tested with a likelihood ratio test (Lynch and Walsh 1998; Bolker et al. 2009), comparing the final model with the random term and using REML to the model without the random factor. The degrees of freedom of all the LRT was always 1 because drop1 compares two models (with and without the tested effect). Sample sizes have been indicated above (section 'Traits' of material and methods), and they have also been noted in the tables regarding the analysis of each response variable.

Amount of variance explained by the final models (R^2 values) was calculated following two different methods depending on the type of models that we fitted for every response variable. For the analyses of the remating interval, the female longevity and the rate of infertile matings, the marginal (i.e., based on just the fixed effects) and conditional (i.e., including random effects) R^2 values for the final LMM or GLMM models were calculated using the function '*sem.model.fits*' implemented in the package '*piecewiseSEM*' (Lefcheck 2016). In the analyses of the total number of matings and the remating proportion, the R^2 values for the final GLMM-PQL models were calculated using the function '*r2beta*' implemented in the package '*r2glmm*' (Jaeger 2017).

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We applied a general protocol for the detection and removal of influential observations and outliers before carrying out the analyses (see Chapter 2). In addition, some other observations were removed a priori due to the fact that these cases lacked information concerning some of the variables included in the models. For the analysis of the rate of infertile matings, two observations were removed from the database because the males escaped from the containers without mating and three other observations were excluded due to the lack of information regarding some variables. 8 observations met the "influential outlier" criteria in this dataset, but we did not exclude them because those observations were those pertaining to females that did not produce offspring, that is, those reflecting the existence of an infertile mating. Thus, the final sample size for the infertile matings dataset was 315 (assay mating focal males to focal females: n = 157 pairs, assay using focal males mated to tester females: n = 158). For the analysis of the number of matings only two females met the "influential outlier" criteria, resulting in a final sample size of 269 females (generation 12: n = 111; generation 30: n = 158). For the analyses of the remating proportion and remating interval, none of the cases was an "influential outlier", but two observations were excluded due to a lack of information, thus the final sample size for this dataset was 269 females (generation 12: n = 112; generation 30: n = 157). Finally, for the female longevity dataset, four observations were excluded because of incomplete information, and 4 additional observations met the "influential outlier" criteria, rendering a final sample size of 263 females after their removal (generation 12: n = 110; generation 30: n = 153). We also run confirmatory analysis including all data to assess whether the inclusion of what we called 'influential outliers' rendered qualitatively different results to those from the main analysis. Results were qualitatively and quantitatively similar before and after the removal of influential outliers and we just show here the results of the main analysis excluding influential outliers, because models pertaining to these analyses meet better the assumptions of normality and homoscedasticity. We checked that the assumptions of the analysis (normality and homogeneity of residuals) were fulfilled by visually inspecting qqplots and plots of the distribution of the residuals against fitted values. We report mean ± standard error values throughout. Tables are provided after the references. Parameter estimates and other details of the models run can be found in the Appendix at the end of the chapter.

Results

Total number of matings

The number of matings was not explained by any of the main factors (selection treatments mating system and population spatial structure) included in the PQL models, its interaction, or female body size (see Table 3.1). However, there was a significant effect of generation, with females from generation 12 having a mean number of matings slightly higher than those from generation 30 (mean ± SE: generation 12: 2.03 ± 0.06; generation 30: 1.86 ± 0.06). Analyses run for each generation separately indicated that the lack of significant effects for the factors

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considered was consistent across generations (see Table 3.2). Table 3.3 shows the mean mating proportion across generations, as well as the number of matings across and within generations for each of the groups analyzed.

Remating proportion

The selection treatments, their interaction, generation or female body size did not explain the propensity of females to remate (see Table 3.4). Table 3.3 shows the mean remating proportion for each of the groups analyzed.

Remating interval

None of the selection treatments or their interaction had a significant effect on remating interval. Neither the female body size, nor the generation affected significantly the results (see table 3.5). The mean remating interval for each of the groups analyzed is shown in Table 3.3.

Female longevity

Neither mating system selection history, population spatial structure selection history, generation, nor the number of matings a female completed influenced female lifespan. Interestingly, a significant interaction between mating system and population spatial structure was found (LRT = 12.74, df = 1, p = 0.0004, Table 3.6 and Fig. 3.2). When females are given multiple opportunities for mating with tester males, females from non-structured polygamous populations live longer than females from non-structured monogamous evolving lines. However, in structured populations the pattern is reversed, with females from monogamous selection regimes living longer than females from polygamous lines. Generation does not have a significant effect (see table 3.6), and indeed the pattern is strongly conserved across generations (Fig. 3.2). The results are not explained by variation in the total number of matings (see table 3.6). Female body size showed a significant and positive correlation with female lifespan (LRT = 20.73, df = 1, p < 0.0001, Fig. 3.3). The larger the female, the longer she lived. Table 3.3 shows the mean female longevity for each of the groups analyzed.

Rate of infertile matings

Only 8 females out of 315 did not produce adult offspring after a single copulation (2.54 % of the total). None of the factors or covariates in the model (selection treatments or their interaction, individuals' body size, age at mating, or whether reproductive output was measured in focal or tester females), had a significant effect on the rates of infertile matings (see table 3.7). Table 3.3 shows the mean ± 1 SE rates of fertile matings for each of the groups analyzed.

Likewise, in the analysis of the fertility threshold (production of less or more than 10 adult offspring after single mating) none of the model terms was significant (see Table 3.8). Female type was marginally significant (LRT = 4.38, df = 1, p = 0.04), with tester females presenting fewer cases in which females did not reach the analytic threshold (10 offspring) (mean ± SE: focal females: 0.94 ± 0.02; tester females: 0.97 ± 0.01), indicating slight differences in fertility due to female origin. These differences may arise due to specific fertility of the particular SHL ID of females used in the focal males mated to tester females assays, or to male-induced

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effects on fertility depending on female origin. In any case this effect did not hold after correction for multiple estimates of probability and we refrain therefore from further interpretations. Female fertility was positively affected by female body size, though this effect was only marginally significant and did not hold after multiple p estimates correction (LRT = 3.90, df = 1, p = 0.05).

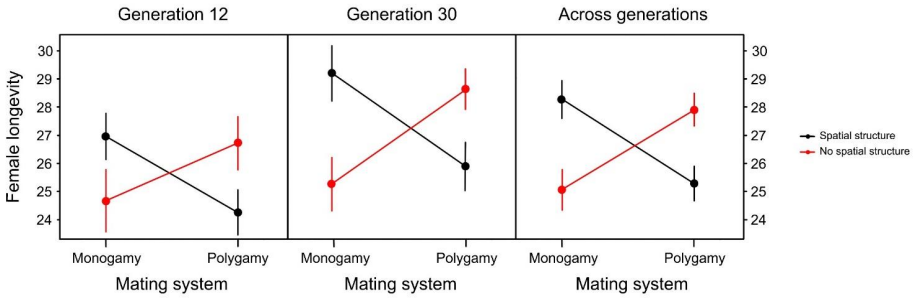

Fig. 3.2 The main and interactive effects of mating system (monogamy vs. polygamy) and spatial population structure (metapopulation structure vs. no structure) selection treatments on female longevity (in days) at generations 12, 30 and across generations. The image depicts the mean (±1SE) lifespan (days) of females exposed to the different mating opportunities for each group calculated across the 4 lines within each selection regime. Data from populations with spatial structure are shown in black while data from populations without spatial structure are shown in red.

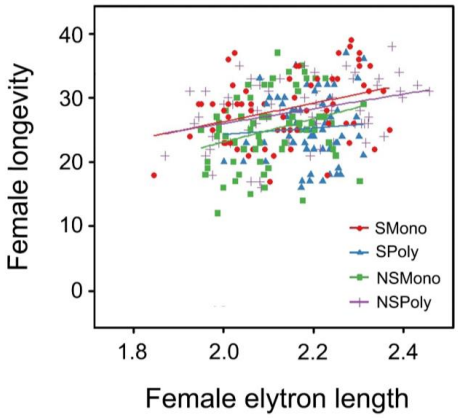

Fig. 3.3. Relationship between female elytron length (in millimeters) and female longevity (in days) for each of the four selection regimes established (resulting from the combination of mating system and population spatial structure selection treatments).

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Discussion

Asymmetries between sexes in relation to the economics of their reproductive behaviour (Parker et al. 1972; Trivers 1972) lead to different evolutionary strategies in males and females (Arnqvist and Rowe 2005). In general, due to their higher reproductive potential, males are expected to maximize their fitness by increasing the number of mates. Females on the other hand, due to the production of lower numbers of gametes compared to males, and their higher parental investment are expected to be choosier and maximize their fitness by mating with one or a few males (Bateman 1948; Trivers 1972; Andersson 1994). Furthermore, mating entails costs (Daly 1978; Chapman et al. 1995; Blanckenhorn et al. 2002), and females normally obtain enough sperm to fertilize all their ova after a single copulation. Then, why is polyandry (female multiple mating behaviour) so widespread across taxa (Arnqvist and Nilsson 2000; Taylor et al. 2014). Disentangling the causes underlying the evolution and maintenance of polyandrous behaviour has been a hot topic for some time now (e.g. Parker 1970; Birkhead et al. 1993; Zeh and Zeh 1996; Yasui 1997; Zeh and Zeh 1997; Yasui 1998; Arnqvist and Nilsson 2000; Birkhead 2000; Jennions and Petrie 2000; Simmons 2001a; Yasui 2001; Hosken and Stockley 2003; Simmons 2003; Garcia-Gonzalez and Simmons 2005; Simmons 2005; Cornell and Tregenza 2007; Garcia-Gonzalez and Simmons 2007; Gowaty 2012; Slatyer et al. 2012; Parker and Birkhead 2013; Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016; McCullough et al. 2017).

This ample body of theoretical and empirical studies collectively suggests that the evolution of polyandrous behaviour depends on the balance between the costs and benefits of multiple mating. Polyandrous females may not only obtain direct benefits (Arnqvist and Nilsson 2000), but also indirect (genetic) benefits that enhance female fitness through the increase of their offspring's fitness, for example by elevating their genetic diversity, viability and/or survival (Yasui 1998; Newcomer et al. 1999; Evans and Magurran 2000; Jennions and Petrie 2000; Garcia-Gonzalez and Simmons 2005; Simmons 2005; Fisher et al. 2006; Garcia-Gonzalez and Simmons 2007, 2011; Garcia-Gonzalez et al. 2015). A separate hypothesis, but also based on the accruement of benefits, for the evolution of female multiple mating suggests that polyandry can be in some situations a risk-spreading bet-hedging strategy. Under this hypothesis polyandrous behavior would serve females to balance out assessment errors in mate choice that may lead to the fertilization of their eggs by unsuitable mates (i.e. low quality, genetically incompatible or infertile males). By mating multiply, females would then reduce the chances of complete reproductive failure compared to monogamous females (for further details see Yasui 1998; Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016; Yasui and Yoshimura 2018).

Ecological and demographical factors such as population size, the number of potential mates, frequencies of suitable and unsuitable mate genotypes, remating costs, or population subdivision are all important factors determining the benefits of multiple mating, and in particular those stemming from a bet-hedging mechanism (see for example Taylor et al. 2014; Garcia-Gonzalez et al. 2015; Holman 2016; Yasui and Garcia-Gonzalez 2016; Yasui and Yoshimura 2018). In particular, however, it is notorious the lack of theoretical and empirical research

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concerning the role of the spatial structuring of populations on the evolution of mating systems in particular, or on sexual selection in general. This is surprising given the well-known importance that metapopulation structure has on many ecological and evolutionary population features (e.g. Hanski 1999; Haikola et al. 2001; Hanski and Gaggiotti 2004; Akçakaya et al. 2007; Gilpin 2013). One of the few explicit studies addressing the connection between population subdivision and the evolution of mating systems was recently carried out by Yasui and Garcia-Gonzalez (2016), who addressed the question from a theoretical point of view. The results in Yasui and Garcia-Gonzalez (2016) study underscored the potential of bet-hedging to provide benefits to polyandrous females in spatially structured populations and the higher probability of fixation of polyandry over monogamy in such populations when the risk of complete reproductive failure as a consequence of mating with unsuitable (e.g., infertile) males is high. Gathering empirical data testing the links between population subdivision and female mating frequency would shed light into the drivers underlying mating system evolution, as well as on the factors moderating the opportunity for sexual selection across the pre- and post-copulatory episodes of sexual selection (see for instance Kvarnemo and Simmons 2013; Evans and Garcia-Gonzalez 2016).

One of our main objectives with our experimental evolution study using the seed beetle *Callosobruchus maculatus* was precisely to get insights into this connection. In this study we have assessed evolutionary divergence in female mating rates and female longevity in response to variation in sexual selection and selection associated to population subdivision (and their interaction). At the same time this assessment provides the first empirical test for some of the predictions derived from the results of Yasui and Garcia-Gonzalez (2016), namely that a history of population spatial structure should favour the evolution of higher female mating rates. This prediction aligns with general expectations from bet-hedging theory applied to the evolutionary stability of multiple mating working as a risk-spreading strategy, which suggests that the success of bet-hedging polyandry is inversely related to population size (Gillespie 1974; Yasui 1998; Hopper 1999; Yasui 2001; Sarhan and Kokko 2007; Starrfelt and Kokko 2012; Holman 2016; Yasui and Garcia-Gonzalez 2016). To the extent that the demes of spatially structured populations are of inferior size that the whole population, bet-hedging benefits (which need to be assessed looking at geometric mean fitness) of female multiple mating depend mainly on the population and subpopulation sizes (the smaller the demes the more likely that there is selection against demographic stochasticity, i.e., the more likely a bet-hedging strategy can succeed), the connectivity among populations (the less connected the more likely bet-hedging is favoured), and the frequency of unsuitable males in the population (the higher the frequency the higher the probability for bet-hedging polyandry to be fixed in the population) (see Yasui and Garcia-Gonzalez 2016). Furthermore, spatial structuring is generally associated to the presence of small demes, where inbreeding is likely, and consequently where it is expected a higher prevalence of fertilization failures, which altogether will promote polyandrous behaviour (Garcia-Gonzalez 2004; Yasui and Garcia-Gonzalez 2016; Bocedi and Reid 2017).

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We found no divergence in female mating rates, female remating propensity or remating interval among the populations from the different selection regimes, even those that differed in population spatial structuring. This may be explained by two main reasons. First, our experimental design enforced 20% migration rates among subpopulations every generation. This migration rate is probably too high, allowing a great deal of gene flow, and therefore preventing to a large extent selection for a bet-hedging strategy (Yasui and Garcia-Gonzalez 2016). According to the results by Yasui and Garcia-Gonzalez (2016), the lower the connectivity between demes the smaller the magnitude of the costs of polyandry that cannot be overcome by bet-hedging derived benefits. In other words, even very low costs of mating would select against the evolution of polyandry via bet-hedging when migration rates among demes are too high. In our design, migration rates were based on logistical constraints and the decision of setting the minimum migration rate for each population involving the two sexes, to avoid sex-specific dispersal effects. This meant that a minimum of one male and a female were transferred (i.e., forced to migrate) from each population to a different one, and this in turn meant a 20% migration rate.

Second, a critical factor favouring the evolution of higher female mating frequencies due to direct benefits or bet-hedging borne benefits is the risk of complete reproductive failure due to male effects such as male infertility, or parental incompatibilities between male and female genotypes (Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016). Our experiments to assess rates of infertile matings revealed that there were no differences in relation to complete reproductive failure risk (or even low fertility risk) among the lines from the selection regimes. In fact, infertility rates were consistently low (around 3%). Bearing in mind the virtually negligible risk of complete mating failure for both monogamous and polygamous populations, together with moderate to high migration rates among subpopulations, it is not surprising perhaps that we did not find divergence in female mating frequencies or remating propensity between populations with or without spatial structuring.

We also failed to find differences in female mating rates between populations with and without sexual selection, a finding against the predictions of sexually antagonistic coevolution or of sexual conflict mediated by ejaculate manipulation (see chapters 5 and 6, and see for instance Pitnick et al. (2001)). On the one hand, males from monogamous males are expected to evolve traits that are less harmful to female fitness, and so females from monogamous lines are expected to be released from selection for the evolution of resistance traits to mating attempts by males. If so, mating rates when females are exposed to standard males would be higher for monogamous females than for polyandrous females. On the other hand, if sexual conflict is mediated by ejaculate manipulation of female refractoriness (i.e., decrease in receptivity leading to increases in remating intervals leading to lower remating rates), by the same token (release of selection for the evolution of female resistance in monogamous females) in this case polygamous females would be expected to exhibit higher mating frequencies when exposed to standard males, compared to monogamous females (see Pitnick et al. 2001). We failed to find

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evidence for any of these possibilities, possibly because in *C. maculatus*, unlike *Drosophila melanogaster*, there seems to be a delicate balance between the benefits and costs implied by the reception of multiple ejaculates, which on the one hand imply higher physical costs of mating, and on the other, hydration benefits (see chapters 4 and 5 and Fox 1993; Arnqvist et al. 2005; Eady et al. 2007; Edvardsson 2007; Ursprung et al. 2009; Yamane and Miyatake 2010a, c). These questions warrant further investigations.

We thus did not find evidence for a response in female mating frequency to the selection treatment. Nonetheless, we detected a remarkable interaction between mating system and population structure selection treatments on female longevity. In populations without spatial structure, females from monogamous populations paid higher costs in terms of longevity than females evolving under the presence of sexual selection (polygamous lines). Since in our experiments all females were mated to standardized males from outside the selection experiment, to avoid covariation due to sexual coevolution to influence the results, our results fit perfectly with the predictions from sexual conflict and sexually antagonistic coevolution regarding the levels of expected evolved female resistance to male induced harm, which should be higher for females from polygamous populations than for females from monogamous populations (see chapters 5 and 6 for further details, and, Holland and Rice 1999; Martin and Hosken 2003; Martin et al. 2004; Gay et al. 2011). However, there was a noteworthy reversal of the longevity patterns expected from sexual conflict theory in spatially structured populations. When populations were subdivided females from polygamous populations died earlier than females from monogamous populations. The analyses controlled for variation in female mating rates, so the results are not explained by such variation (which in any case was statistically non-significant). The intriguing evolutionary pattern of reversal in longevity was consistent across generations, proving that such result was not a mere artefact (and see Chapters 5 and 6). Our results do not shed light into the precise mechanisms explaining this reversal, but the results unambiguously point towards the fact sexual selection and associated effects (e.g., sexual conflict adaptations and sexual coevolutionary dynamics) are moderated by spatial population subdivision. The evolutionary and ecological implications of this would be paramount, and so further investigations into the precise mechanisms underlying our findings and in general on the consequences of metapopulation structure for sexual selection would advance the field significantly.

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Table 3.1. Analysis of the number of matings across generations. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. These values correspond to the outputs of the full and minimal PQL models. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: $R^2 = 0.02$.

Full model					
Effect	**Estimate**	**SE**	**df**	**t**	**p**
Intercept	-0.26	0.19	251	-1.37	**< 0.0001**
Mating system : structure	-1.78	0.13	12	-13.89	0.20
Mating system	0.13	0.14	12	0.97	0.35
Structure	0.18	0.14	12	1.34	0.20
Generation	0.01	0.003	251	1.95	0.0521
Female elytron length	-0.05	0.30	251	-0.17	0.86
Minimal model					
Intercept	-1.71	0.11	252	-15.73	**< 0.0001**
Mating system	-0.001	0.10	13	-0.02	0.98
Structure	0.054	0.10	13	0.53	0.60
Generation	0.007	0.003	252	2.35	**0.02**

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Table 3.2. Analyses of the number of matings for each generation assayed. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. These values correspond to the outputs of the full and minimal PQL models. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: generation 12 (R^2= 0.02), generation 30 (R^2= 0.004).

Generation 12					
Full model					
Effect	Estimate	SE	df	t	p
Intercept	-1.57	0.13	94	-11.73	**<0.0001**
Mating system : structure	0.04	0.24	12	0.18	0.86
Mating system	0.09	0.19	12	-0.48	0.64
Structure	0.09	0.14	12	0.60	0.56
Female elytron length	0.44	0.63	94	0.70	0.49
Minimal model					
Intercept	-1.62	0.09	95	-19.01	**<0.0001**
Mating system	-0.03	0.1	13	-0.33	0.75
Structure	0.08	0.1	13	0.77	0.45
Generation 30					
Full model					
Effect	Estimate	SE	df	t	p
Intercept	-1.65	0.14	141	-11.83	**<0.0001**
Mating system : structure	-0.47	0.28	12	-1.70	0.12
Mating system	0.25	0.19	12	1.31	0.21
Structure	0.27	0.19	12	1.40	0.19
Female elytron length	0.20	0.44	141	0.46	0.65
Minimal model					
Intercept	-1.52	0.12	142	-12.22	**<0.0001**
Mating system	0.02	0.14	13	0.17	0.87
Structure	0.04	0.14	13	0.25	0.81

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Table 3.3. Means ± 1 SE and sample size (within brackets) for the proportion of fertile matings (measured at generation 34 of the selection protocol) and for each of the remaining response variables analysed (generations 12 and 30; statistics are given across generations except for number of matings because the opportunities for mating differed between the two generations assayed (see text)). The data is given for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation), as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). [a] Note that longevity is substantially higher for females in these assays compared to other longevity estimates of female *Callosobruchus maculatus* (for instance in Chapters 2 and 5) because in the present study females were not allowed to oviposit.

Trait	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Fertile matings	0.97 ± 0.02 (78)	0.95 ± 0.02 (79)	0.99 ± 0.01 (80)	0.99 ± 0.01 (78)	0.98 ± 0.01 (158)	0.97 ± 0.01 (157)	0.96 ± 0.02 (157)	0.99 ± 0.01 (158)
Number of matings (across generations)	1.79 ± 0.09 (68)	1.98 ± 0.09 (68)	2.07 ± 0.08 (67)	1.86 ± 0.08 (66)	1.93 ± 0.06 (135)	1.93 ± 0.06 (134)	1.89 ± 0.06 (136)	1.97 ± 0.06 (133)
Number of matings (generation 12)	1.96 ± 0.12 (28)	1.96 ± 0.14 (28)	2.14 ± 0.12 (28)	2.04 ± 0.14 (27)	2.05 ± 0.09 (56)	2.00 ± 0.1 (55)	1.96 ± 0.09 (56)	2.09 ± 0.09 (55)
Number of matings (generation 30)	1.68 ± 0.13 (40)	2.00 ± 0.11 (40)	2.03 ± 0.11 (39)	1.74 ± 0.10 (39)	1.85 ± 0.09 (79)	1.87 ± 0.08 (79)	1.84 ± 0.09 (80)	1.88 ± 008 (78)
Mating proportion (across generations)	0.17 ± 0.009 (68)	0.19 ± 0.008 (68)	0.19 ± 0.008 (67)	0.17 ± 0.008 (66)	0.18 ± 0.006 (135)	0.18 ± 0.006 (134)	0.18 ± 0.006 (136)	0.18 ± 0.005 (133)
Remating proportion	0.08 ± 0.01 (67)	0.10 ± 0.01 (68)	0.11 ± 0.01 (67)	0.09 ± 0.01 (67)	0.10 ± 0.01 (134)	0.10 ± 0.01 (135)	0.09 ± 0.01 (135)	0.10 ± 0.01 (134)
Remating Interval (days)	6.35 ± 0.44 (67)	5.82 ± 0.41 (68)	4.73 ± 0.35 (67)	5.90 ± 0.44 (67)	5.54 ± 0.29 (134)	5.86 ± 0.30 (135)	6.09 ± 0.30 (135)	5.31 ± 0.29 (134)
Female longevity (days)[a]	28.20 ± 0.66 (64)	25.25 ± 0.61 (67)	25.03 ± 0.71 (64)	27.84 ± 0.58 (68)	26.62 ± 0.51 (128)	26.55 ± 0.44 (135)	26.69 ± 0.47 (131)	26.48 ± 0.47 (132)

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Table 3.4. Analysis of propensity to remate (remating proportion) across generations. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: R^2= 0.01.

Full model					
Effect	**Estimate**	**SE**	**df**	**t**	**p**
Intercept	-2.47	0.19	251	-12.78	**<0.0001**
Mating system : structure	-0.46	0.35	12	-1.33	0.21
Mating system	0.25	0.25	12	1.02	0.33
Structure	0.35	0.25	12	1.41	0.18
Generation	0.04	0.12	251	0.31	0.76
Female elytron length	-0.16	0.57	251	0.29	0.77
Minimal model					
Intercept	-2.33	0.16	253	-14.61	**<0.0001**
Mating system	0.01	0.18	13	0.07	0.94
Structure	0.12	0.18	13	0.68	0.51

Table 3.5. Analysis of remating interval across generations. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal R^2= 0.02; conditional R^2= 0.11).

Effect	LRT	p
Mating system : structure	1.82	0.18
Mating system	0.23	0.63
Structure	1.35	0.25
Generation	0.41	0.52
Female elytron length	0.08	0.78
Line (Random)	10.80	**0.001**

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Table 3.6. Analysis of female longevity across generations. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal R^2= 0.14; conditional R^2= 0.15).

Effect	LRT	p
Mating system : structure	12.74	**0.0004**
Mating system	0.60	0.44
Structure	0.01	0.92
Generation	0.11	0.74
Female elytron length	20.73	**<0.0001**
Total number of matings	0.20	0.65
Line (Random)	0.28	0.60

Table 3.7. Analysis of rates of infertile matings. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal R^2= 0.11; conditional R^2= 0.11.

Effect	LRT	p
Mating system : structure	0.17	0.68
Mating system	0.52	0.47
Structure	2.15	0.14
Male elytron length	0.83	0.36
Female elytron length	0.66	0.42
Male age	0.29	0.59
Female age	0.12	0.73
Female type	0.51	0.47
Line (Random)	0	1

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Table 3.8. Analysis of fertility threshold (production of less or more than 10 adult offspring after single mating). The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal R^2= 0.13; conditional R^2= 0.20.

Effect	LRT	p
Mating system : structure	1.41	0.24
Mating system	0.02	0.88
Structure	0.06	0.80
Male elytron length	0.51	0.47
Female elytron length	3.90	0.05
Male age	0.42	0.52
Female age	0.08	0.78
Female type	4.38	0.04
Line (Random)	0.29	0.59

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Appendix Chapter 3

Model: Analysis of infertile mating rate

Full model

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]
Family: binomial(logit). Formula: adults ~ ss + structure + ss:structure + centfel + centmel +
centmaleage + centfemaleage + femaletype + (1 | line)
     AIC      BIC   logLik deviance df.resid
    87.4    124.9    -33.7     67.4      305
Scaled residuals:
     Min       1Q   Median       3Q      Max
-12.6228   0.0868   0.1206   0.1819   0.4323
Random effects:
 Groups Name        Variance Std.Dev.
 line   (Intercept) 0        0
Number of obs: 315, groups:  line, 16
Fixed effects:
                      Estimate Std. Error z value Pr(>|z|)
(Intercept)             2.3775     1.4548   1.634    0.102
sspoly                 -0.8116     0.9183  -0.884    0.377
structurenometa         0.6302     1.2646   0.498    0.618
centfel                 6.3697     4.8516   1.313    0.189
centmel                -5.3439     5.1334  -1.041    0.298
centmaleage             0.8725     1.1566   0.754    0.451
centfemaleage          -0.7959     0.9894  -0.804    0.421
femaletypetester        3.1832     2.9185   1.091    0.275
sspoly:structurenometa  0.9957     1.7249   0.577    0.564
```

Minimal model

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]
Family: binomial (logit). Formula: adults ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
    79.9     94.9    -35.9     71.9      311
Scaled residuals:
     Min       1Q   Median       3Q      Max
-10.2191   0.0979   0.1272   0.1720   0.2235
Random effects:
 Groups Name        Variance Std.Dev.
 line   (Intercept) 0        0
Number of obs: 315, groups:  line, 16
Fixed effects:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)       3.5205     0.6215   5.664 1.48e-08 ***
sspoly           -0.5239     0.7415  -0.707    0.480
structurenometa   1.1280     0.8250   1.367    0.172
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Analysis of fertility (more than 10 offspring)

Full model

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]
Family: binomial(logit). Formula: tenadults ~ ss + structure + ss:structure + centfel + centmel +
centmaleage + centfemaleage + femaletype + (1 | line)
     AIC      BIC   logLik deviance df.resid
   119.9    157.4    -50.0     99.9      305
Scaled residuals:
    Min      1Q  Median      3Q     Max
-7.1443  0.1177  0.1630  0.2192  0.5826
```


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```
Random effects:
 Groups Name        Variance Std.Dev.
 line   (Intercept) 0.1533   0.3915
Number of obs: 315, groups:  line, 16
Fixed effects:
                       Estimate Std. Error z value Pr(>|z|)
(Intercept)            3.550203   0.008001   443.7   <2e-16 ***
sspoly                -0.906271   0.007998  -113.3   <2e-16 ***
structurenometa       -0.937465   0.007999  -117.2   <2e-16 ***
centfel                7.013493   0.007996   877.1   <2e-16 ***
centmel                1.880440   0.007996   235.2   <2e-16 ***
centmaleage            0.699468   0.007996    87.5   <2e-16 ***
centfemaleage          0.073034   0.007994     9.1   <2e-16 ***
femaletypetester       1.103194   0.007998   137.9   <2e-16 ***
sspoly:structurenometa 1.408149   0.007997   176.1   <2e-16 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]
Family: binomial (logit). Formula: tenadults ~ ss + structure + centfel + femaletype + (1 | line)
     AIC      BIC   logLik deviance df.resid
   114.0    136.5    -51.0    102.0      309
Scaled residuals:
    Min      1Q  Median      3Q     Max
-6.3522  0.1261  0.1626  0.2234  0.4948
Random effects:
 Groups Name        Variance Std.Dev.
 line   (Intercept) 0.3016   0.5492
Number of obs: 315, groups:  line, 16

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)        2.96474    0.67253   4.408 1.04e-05 ***
sspoly            -0.09724    0.66016  -0.147   0.8829
structurenometa   -0.16106    0.64980  -0.248   0.8042
centfel            7.46978    3.76551   1.984   0.0473 *
femaletypetester   1.35377    0.68431   1.978   0.0479 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Evolution of number of matings across generations

Full model

```
Linear mixed-effects model fit by maximum likelihood

  AIC BIC logLik

   NA  NA     NA
Random effects:
 Formula: ~1 | line
        (Intercept)  Residual
StdDev:   0.1623789 0.5185656
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: cbind(total, fails) ~ ss + structure + ss:structure + gen + centfel
                            Value  Std.Error  DF    t-value p-value
(Intercept)            -1.7836296 0.12839158 251 -13.892107  0.0000
sspoly                  0.1337016 0.13825637  12   0.967056  0.3526
structurenometa         0.1840508 0.13699624  12   1.343473  0.2040
gen                     0.0070572 0.00361572 251   1.951814  0.0521
centfel                -0.0526176 0.29706457 251  -0.177125  0.8596
sspoly:structurenometa -0.2649045 0.19345924  12  -1.369304  0.1960
```


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```
 Correlation:
                        (Intr) sspoly strctr gen    centfl
sspoly                  -0.594
structurenometa         -0.515  0.493
gen                     -0.650  0.085 -0.035
centfel                  0.427 -0.139  0.061 -0.616
sspoly:structurenometa  0.390 -0.703 -0.705 -0.012  0.016
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.38546015 -0.58740382  0.01306874  0.48204720  2.89857699
Number of Observations: 269
Number of Groups: 16
```

Minimal model

```
Linear mixed-effects model fit by maximum likelihood
  AIC BIC logLik
   NA  NA     NA
Random effects:
 Formula: ~1 | line
        (Intercept)  Residual
StdDev:   0.1753652 0.5184273
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: cbind(total, fails) ~ ss + structure + gen
                     Value  Std.Error  DF    t-value p-value
(Intercept)     -1.7078598 0.10855665 252 -15.732430  0.0000
sspoly          -0.0017628 0.10195507  13  -0.017290  0.9865
structurenometa  0.0538292 0.10195511  13   0.527970  0.6064
gen              0.0066584 0.00283768 252   2.346419  0.0197
 Correlation:
                (Intr) sspoly strctr
sspoly          -0.473
structurenometa -0.476  0.010
gen             -0.578 -0.002  0.001
Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.3873554 -0.5903248 -0.0297477  0.4702995  2.8132729
Number of Observations: 269
Number of Groups: 16
```

Model: Evolution of number of matings per generation

Generation 12

Full model

```
Linear mixed-effects model fit by maximum likelihood
  AIC BIC logLik
   NA  NA     NA
Random effects:
 Formula: ~1 | line
        (Intercept) Residual
StdDev:   0.1332804 0.488777
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: cbind(total, fails) ~ ss + structure + ss:structure + centfel
                            Value Std.Error DF    t-value p-value
(Intercept)            -1.5689169 0.1336990 94 -11.734696  0.0000
sspoly                 -0.0889973 0.1860052 12  -0.478467  0.6409
structurenometa         0.0854130 0.1428660 12   0.597854  0.5611
```


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```
centfel                 0.4418023 0.6332592 94   0.697664  0.4871
sspoly:structurenometa  0.0432517 0.2427833 12   0.178149  0.8616
 Correlation:
                       (Intr) sspoly strctr centfl
sspoly                 -0.831
structurenometa        -0.639  0.487
centfel                 0.659 -0.645 -0.166
sspoly:structurenometa  0.684 -0.812 -0.666  0.565
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.76458527 -0.30132865 -0.07079474  0.45768590  2.33997897
Number of Observations: 111
Number of Groups: 16
```

Minimal model

```
Linear mixed-effects model fit by maximum likelihood
  AIC BIC logLik
   NA  NA     NA
Random effects:
 Formula: ~1 | line
        (Intercept)  Residual
StdDev:   0.1291522 0.4911128
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: cbind(total, fails) ~ ss + structure
                     Value  Std.Error DF    t-value p-value
(Intercept)     -1.6170434 0.08506229 95 -19.010109  0.0000
sspoly          -0.0319076 0.09802804 13  -0.325494  0.7500
structurenometa  0.0757299 0.09802653 13   0.772545  0.4536
 Correlation:
                (Intr) sspoly
sspoly          -0.574
structurenometa -0.586  0.007
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.69948618 -0.33864344 -0.08910289  0.44078817  2.35634444
Number of Observations: 111
Number of Groups: 16
```

Generation 30

Full model

```
Linear mixed-effects model fit by maximum likelihood
  AIC BIC logLik
   NA  NA     NA
Random effects:
 Formula: ~1 | line
        (Intercept)  Residual
StdDev:   0.2263938 0.5099163
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: cbind(total, fails) ~ ss + structure + ss:structure + centfel
                            Value Std.Error  DF    t-value p-value
(Intercept)            -1.6453147 0.1391149 141 -11.827016  0.0000
sspoly                  0.2484703 0.1893819  12   1.312007  0.2141
structurenometa         0.2699398 0.1922773  12   1.403909  0.1857
centfel                 0.2036533 0.4418049 141   0.460957  0.6455
sspoly:structurenometa -0.4669193 0.2751382  12  -1.697036  0.1155
```


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```
 Correlation:
                      (Intr) sspoly strctr centfl
sspoly                -0.710
structurenometa       -0.725  0.514
centfel               -0.242  0.075  0.181
sspoly:structurenometa  0.534 -0.703 -0.719 -0.240
Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.2531507 -0.6061590 -0.0864642  0.6538332  2.7464955
Number of Observations: 158
Number of Groups: 16
```

Minimal model

```
Linear mixed-effects model fit by maximum likelihood
  AIC BIC logLik
   NA  NA     NA
Random effects:
 Formula: ~1 | line
        (Intercept)  Residual
StdDev:   0.2497549 0.5105622
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: cbind(total, fails) ~ ss + structure
                     Value Std.Error  DF    t-value p-value
(Intercept)     -1.5206573 0.1244836 142 -12.215725  0.0000
sspoly           0.0245132 0.1429862  13   0.171437  0.8665
structurenometa  0.0354626 0.1429857  13   0.248015  0.8080
 Correlation:
                (Intr) sspoly
sspoly          -0.584
structurenometa -0.582  0.013
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.28425046 -0.65311165 -0.08393352  0.68920502  2.84321323
Number of Observations: 158
Number of Groups: 16
```

Model: Evolution of remating proportion across generations

Full model

```
Linear mixed-effects model fit by maximum likelihood
  AIC BIC logLik
   NA  NA     NA
Random effects:
 Formula: ~1 | line
        (Intercept)  Residual
StdDev:   0.2807148 0.7254535
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: cbind(remat, noremat) ~ ss + structure + ss:structure + gen +      centfel
                             Value Std.Error  DF    t-value p-value
(Intercept)            -2.4682055 0.1930949 251 -12.782345  0.0000
sspoly                  0.2540364 0.2497863  12   1.017015  0.3292
structurenometa         0.3475124 0.2459483  12   1.412949  0.1831
gen30                   0.0378274 0.1231552 251   0.307152  0.7590
centfel                -0.1643837 0.5667954 251  -0.290023  0.7720
sspoly:structurenometa -0.4607568 0.3461834  12  -1.330962  0.2079
```


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```
Correlation:
                        (Intr) sspoly strctr gen30  centfl
sspoly                  -0.698
structurenometa         -0.647  0.505
gen30                   -0.387  0.092 -0.038
centfel                  0.285 -0.158  0.057 -0.612
sspoly:structurenometa  0.479 -0.709 -0.706 -0.013  0.031
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.69574314 -0.92764952  0.03881547  0.49087561  3.33736792
Number of Observations: 269
Number of Groups: 16
```

Minimal model

```
Linear mixed-effects model fit by maximum likelihood
  AIC BIC logLik
   NA  NA     NA
Random effects:
 Formula: ~1 | line
        (Intercept)  Residual
StdDev:   0.3040093 0.7245284
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: cbind(remat, noremat) ~ ss + structure
                     Value Std.Error  DF    t-value p-value
(Intercept)     -2.3293179 0.1594524 253 -14.608231  0.0000
sspoly           0.0129211 0.1816579  13   0.071129  0.9444
structurenometa  0.1239949 0.1816745  13   0.682511  0.5069
 Correlation:
                (Intr) sspoly
sspoly          -0.585
structurenometa -0.590  0.020
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.69131722 -0.93679324 -0.00148381  0.47055410  3.24404175
Number of Observations: 269
Number of Groups: 16
```

Model: Evolution of remating interval across generations

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Rremintmin ~ ss + structure + ss:structure + centfel + gen + (1 | line)
     AIC      BIC   logLik deviance df.resid
   595.6    624.3   -289.8    579.6      261
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.4398 -0.7312 -0.1054  0.9242  2.2187
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.04541  0.2131
 Residual             0.47700  0.6907
Number of obs: 269, groups:  line, 16
Fixed effects:
                       Estimate Std. Error        df t value Pr(>|t|)
(Intercept)             2.35226    0.15167  24.50000  15.509 3.57e-14 ***
sspoly                 -0.08721    0.19398  16.52000  -0.450    0.659
structurenometa        -0.33563    0.19289  16.15000  -1.740    0.101
centfel                -0.14498    0.48882 263.08000  -0.297    0.767
gen30                   0.08578    0.10877 257.91000   0.789    0.431
```


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```
sspoly:structurenometa   0.32705    0.27165  15.89000   1.204    0.246
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Rremintmin ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
   591.6    609.6   -290.8    581.6      264
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.3877 -0.7923 -0.1265  0.9083  2.1249
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.05173  0.2275
 Residual             0.47839  0.6917
Number of obs: 269, groups:  line, 16
Fixed effects:
                Estimate Std. Error       df t value Pr(>|t|)
(Intercept)      2.32237    0.12268 15.85900  18.930 2.61e-12 ***
sspoly           0.06793    0.14160 15.83100   0.480    0.638
structurenometa -0.16759    0.14160 15.83100  -1.184    0.254
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Evolution of female longevity across generations

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: longev ~ ss + structure + ss:structure +centtotal+centfel+gen+(1|line)
     AIC      BIC   logLik deviance df.resid
  1607.0   1639.2   -794.5   1589.0      254
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.38479 -0.68555 -0.01118  0.69326  2.33371
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)  0.2158  0.4645
 Residual             24.4302  4.9427
Number of obs: 263, groups:  line, 16
Fixed effects:
                      Estimate Std. Error       df t value Pr(>|t|)
(Intercept)            28.5574     0.8142  36.3000  35.072  < 2e-16 ***
sspoly                 -3.7346     0.9489  17.4100  -3.936 0.001024 **
structurenometa        -2.7423     0.9469  17.3300  -2.896 0.009907 **
centtotal              -0.2146     0.4278 231.2000  -0.502 0.616357
centfel                13.5145     3.4841 261.5600   3.879 0.000133 ***
gen30                  -0.3082     0.7884 255.0500  -0.391 0.696205
sspoly:structurenometa   5.7601     1.3158  16.1900   4.378 0.000457 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: longev ~ ss + structure + ss:structure + centfel + (1 | line)
     AIC      BIC   logLik deviance df.resid
  1603.4   1628.4   -794.7   1589.4      256
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.39074 -0.68542  0.00158  0.70410  2.37191
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)  0.30    0.5477
 Residual             24.39    4.9387
```


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```
Number of obs: 263, groups:  line, 16
Fixed effects:
                        Estimate Std. Error       df t value Pr(>|t|)
(Intercept)              28.4031     0.6769  17.3400  41.963  < 2e-16 ***
sspoly                   -3.7374     0.9613  17.6100  -3.888 0.001116 **
structurenometa          -2.8304     0.9582  17.4700  -2.954 0.008697 **
centfel                  12.7629     2.7435 258.5900   4.652 5.25e-06 ***
sspoly:structurenometa    5.8473     1.3363  16.5400   4.376 0.000437 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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Chapter 4

Assessing the effects of sexual selection and population spatial structure on population viability: an experimental evolution approach

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Assessing the effects of sexual selection and population spatial structure on population viability: an experimental evolution approach.

Eduardo Rodriguez-Exposito [1] and Francisco Garcia-Gonzalez [1,2]

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Abstract

The viability of a population ultimately determines whether populations persist through time. Population viability is influenced by several factors among which sexual selection stands out because it can lead to faster adaptation, facilitate the removal of deleterious alleles and/or reduce inbreeding depression, and consequently reduce the probability of population extinction. According to a recent theoretical study, population persistence over time is contingent on the interactive effects of mating system and the level of population spatial structuring and the connectivity among subpopulations. Empirical tests for these ideas are, however, lacking. In this study we have implemented an experimental evolution approach using the seed beetle *Callosobruchus maculatus* to assess the viability of populations evolving under four different selection regimes. These selection regimes are the result of the combination of two levels of mating system (monogamy vs. polygamy) and population spatial structure (structure vs. no structure) selection treatments. To estimate the viability of our populations, we gauged two demographical parameters that influence population viability: population productivity (number of adult offspring produced in the population), including lifetime reproductive success, LRS, across the females of the population, and female longevity. In general, neither the mating system, nor the population spatial structure or their interaction had a significant effect on productivity, except for an effect of population subdivision selection history on short-term productivity detected after 47 generations. Specifically, spatially structured populations (metapopulations) produced fewer offspring than their undivided counterparts. The analysis of female longevity yielded results in concordance with the predictions of sexual conflict theory. Females from polygamous populations lived less than their monogamous counterparts, probably as a reflection of the higher male-induced costs that these females face, or the higher investment into resistance traits, which could trade-off with female survival. A positive relationship between female body weight and female longevity was detected. Finally, a noticeable interaction between mating system and population spatial structure was found affecting female longevity at generation 47. This result provides the first empirical proof that the effects of sexual conflict can be altered by population spatial structure and that this entails far-reaching implications for population viability.

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Introduction

The viability of a population is a key attribute that ultimately determines the populations' ability to persist through time and to elude extinction. Population viability is determined by factors such as birth and mortality rates, and is contingent on both genetic and environmental sources of variance (Turchin 2003).

In recent times there has been increasing interest on whether and how population viability (or population productivity as a proxy of it) is influenced by sexual selection (e.g. Holland and Rice 1999; Agrawal 2001; Martin and Hosken 2003; Whitlock and Agrawal 2009; Plesnar-Bielak et al. 2012; Grieshop et al. 2016). It has been suggested that sexual selection, as well as female multiple mating (polyandry), can lead to faster adaptation, facilitate the removal of deleterious alleles and/or reduce inbreeding depression, and therefore reduce the probability of population extinction (Tregenza and Wedell 2002; Whitlock and Agrawal 2009; Jarzebowska and Radwan 2010; Holman and Kokko 2013). Polyandry is known to enhance female reproductive success not only through direct or material benefits (e.g. Arnqvist and Nilsson 2000; Simmons 2001; Hasson and Stone 2009) but also through indirect (i.e., genetic) benefits (Yasui 1997, 1998; Jennions and Petrie 2000; Tregenza and Wedell 2000; Zeh and Zeh 2001; Kempenaers 2007; Yasui and Garcia-Gonzalez 2016). Importantly, recent studies have also explicitly linked polyandry to an increase in population viability and a consequent reduction of extinction rates (Price et al. 2010; Wade 2010; Power and Holman 2014; Yasui and Garcia-Gonzalez 2016). However, sexual conflict, or the divergent evolutionary interests of males and females (Parker 1979; Arnqvist and Rowe 2005; Rice and Gavrilets 2014), and its associated costs, add complexity to our understanding of the evolutionary trajectories of population viability under sexual selection (Arnqvist and Rowe 2005; Whitlock and Agrawal 2009).

Experimental evolution studies manipulating mating system (and hence the presence or intensity of sexual selection, and of sexual conflict, if prevalent in the system studied) have shed light on the links between sexual selection and population viability (Holland and Rice 1999; Martin and Hosken 2003; Crudgington et al. 2010; Hollis and Houle 2011; Arbuthnott and Rundle 2012; Almbro and Simmons 2014; Lumley et al. 2015). For instance, the classical study by Holland and Rice (1999) on *Drosophila melanogaster* showed that populations evolving under enforced monogamy (in absence of sexual selection and sexual conflict) exhibited greater net reproductive rates than polyandrous selection lines (where sexual selection and sexual conflict was present). These detrimental effects of sexual selection on population fitness are attributable to sexual conflict, with more competitive males imposing higher costs to female reproductive success (Holland and Rice 1999; and see Hollis and Houle 2011). Higher fitness in monogamous compared to polyandrous populations were also found by Martin et al. (2004) in another dipteran species, *Scatophaga stercoraria*. Martin and Hosken (2003) found divergence in fecundity between monogamous and polygamous selection lines of another species, *Sepsis cynipsea*. In this case, however, there were no significant differences in lifetime reproductive success between the two selection regimes. More recently Lumley et al. (2015) have shown in the beetle *Tribolium castaneum* that lineages derived from populations experimentally evolved under the absence of sexual selection experienced higher extinction

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probabilities under inbreeding than lineages from populations experiencing a history of sexual selection. In sum, whether polyandry (and sexual selection) impacts positively or negatively on population fitness remains a hot question in evolutionary biology (Holman and Kokko 2013; Martinossi-Allibert et al. 2018).

Interestingly, recent findings suggest that mating system evolution, and the influence of mating system on population persistence over time (i.e., extinction rates) are contingent on the level of population subdivision and the connectivity of subpopulations (Yasui and Garcia-Gonzalez 2016). Populations are frequently divided in demes that are more or less separated and interconnected, i.e., what is known as metapopulations (Levins 1969; Hanski and Gilpin 1991; Hanski 1998; Hanski 1999). Classical metapopulation theory initially developed by Levins (1970) overlooked the connection between metapopulation structure and extinction dynamics (Molofsky and Ferdy 2005). Notwithstanding, a large body of research over the last decades has been devoted to expand and improve the theory of metapopulation ecology and evolution (Hanski and Gilpin 1991; Hastings and Harrison 1994; Hanski 1999; Molofsky and Ferdy 2005; Eriksson et al. 2014), and the finite lifetime of metapopulations has been explicitly acknowledged for some time now (Hanski and Gilpin 1991).

It is currently accepted that population spatial structure is an important factor mediating population viability and the population's probability of extinction (Hanski 1998; Saccheri et al. 1998; Hanski 1999; Haikola et al. 2001; Nieminen et al. 2001; Hanski and Gaggiotti 2004; Akçakaya et al. 2007; Gilpin 2013). A large number of studies have determined the factors that promote the local extinction of metapopulation demes, for instance, large interpopulation distances (Sjögren 1991; Molofsky and Ferdy 2005), low levels of heterozygosity (Saccheri et al. 1998; Hartl and Clark 2007), migration flow (Richards 2000 and references therein; Eriksson et al. 2014 but see Molofsky and Ferdy 2005) and, critically, a small population size (Haikola et al. 2001; Caballero et al. 2017). In small populations, the possibilities for selection to operate are limited, and higher mutation loads may lead to inbreeding depression and associated negative effects, such as an increase in development times and a decrease in offspring survival, and consequently a drop in the net reproductive success of the individuals (Harano 2011); all this would ultimately decrease population viability, opening the gates for population extinction. It is easy therefore to understand why small populations are more prone to extinction simply due to stochastic processes (Martínez-Ruiz and Knell 2017). In addition, it is important to bear in mind that in small or fragmented populations the number of available mates is limited and a fraction of those, as it happens in populations of any size, would be sterile or genetically incompatible as sexual partners (Zeh and Zeh 1996; Garcia-Gonzalez 2004). Importantly, in small populations or populations with spatial structure, the risk of female reproductive failure as a consequence of higher probabilities of encountering (and mating with) unsuitable males is higher. This fact may lead to selection for female multiple mating because polyandrous behaviour, working as a risk-spreading bet-hedging strategy, would minimize the detrimental consequences of mating with unsuitable males (Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016), and this in turn would decrease the probability of extinction (Yasui and Garcia-Gonzalez 2016).

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In summary, both sexual selection and the spatial structure of demes are important factors determining the fate of a population. It is striking, however, that experimental evolution studies have so far overlooked the potentially pivotal role of population spatial structure on population viability. In this study we fill this gap, innovatively exploiting the power of experimental evolution to carry out, for the first time, empirical investigations on the influence of both sexual selection and population spatial structure, as well as its interaction, on population viability.

Material and methods

The methodology followed to create the experimentally evolved populations in our selection experiment has been described in detail in Chapter 1 (The Experimental Evolution Approach section). Additionally, basic information regarding the biology of our study model (Study Animals section) and the source population (Stock Population section) has been provided in Chapter 1.

Below we describe the methods followed to assess the viability of the replicated lines evolving under the four separate selection regimes resulting from the combination of the mating system selection treatment (two levels: monogamy vs. polygamy) and the population spatial structure selection treatment (two levels: presence or absence of population subdivision).

Traits

Two main response variables were measured (i) the total number of adults (productivity) produced from one generation to the next, at the population level and by a constant number of females (see below), and (ii) female longevity after exposure to matings and male harassment for 48 hours.

Productivity

Two different and complementary measurements of productivity were carried out. For the first measurement, henceforth STP (short-term productivity), the number of adults produced by the 25 breeding females in each of our 16 replicated lines was counted. For the second measurement of productivity, henceforth LTP (long-term productivity), we used 10 pairs of breeders from each replicate line.

The size of the vials where the experimental individuals were placed and the number of beans (oviposition substrate) in the containers varied depending on the productivity measure. Our aim was to keep the number of beans per female ratio constant regardless of the conditions. In this way, the breeders (n = 50) in our selection lines, from which our STP measure is obtained, were housed as follows (see also Chapter 1): NSPoly individuals were in a 750 ml plastic container with 1600 beans approx., SPoly individuals were distributed in five medium size containers (140 ml; 320 beans approx. in each), and each male-female pair from the NSMono and SMono selection lines was in a small size container (30 ml, 65 beans approx.). For the LTP measure, the number of beans added to the large 750 ml container (individuals from NSPoly lines) was reduced (640 beans approx.) to maintain constant the number of beans per female, since in this productivity measure the number of females was 10 instead of 25. The dimensions of containers and the number of beans for the experimental animals drawn from the

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other selection lines was the same as for the short-term productivity measure, but the number of containers per group was reduced to accommodate 10 instead of 25 reproducing females (i.e., for females from SPoly lines, two 140 ml containers were used, each housing 5 females, and for each NSMono and SMono line 10 small containers were used instead of 25).

Sex ratio was always constant at 1:1 regardless of the experimental group. For STP, males and females were housed together for 48 hours in their respective containers (see above) with beans, and then removed from the containers where the eggs were laid, which were kept under laboratory conditions (see section Stock Populations in Chapter 1) for an additional 29 days period, after which the vials were frozen. For LTP, males and females were housed together in a first container with beans for 24 hours (day 1). On day 2, individuals were transferred to a second container with beans for 24 hours. On day 3, the males were removed and the females were left in the container with beans for other 24 hours, after which they were transferred to a third container with beans. Females remained in this container until they died. Again, vials were frozen 29 days after the placement of the female in the third container. In both STP and LTP measures, the vials with offspring were frozen 30 days after the removal of the breeding males, for subsequent counting of the number of adults produced. Due to development times under our laboratory conditions (average of 21-24 days to complete the cycle from egg to adult), and taking into account that females lay most of their eggs soon after the last copulation, and typically within the following few days (e.g., 90% of the lifetime offspring production by females is attributable to oviposition within the first three days after mating; Zajitschek et al. in press, and see also Credland and Wright 1989), a period of 30 days is long enough to ensure that most, if not all, the offspring complete development and emerge as adults from the beans when the vials were frozen for later counting. Figure 4.1 provides an outline of the two productivity measures.

The two measurements of productivity differed basically in two main details: the number of breeders and the period of time that the females had to lay eggs. For the STP measure, male-female cohabitation lasted 48 hours, and this was the period for oviposition too. For the LTP measure, females were also housed with males for 48 hours, but afterwards the males were removed and the females remained in the containers with substrate to lay eggs until they died. LTP measure was therefore a proxy for productivity that is based on the lifetime reproductive success (LRS) measures of the sampled females.

STP was measured after 11, 14, 19, 22, 26, 46 and 47 generations of evolution under the different selection treatments. LTP was measured after 11, 46 and 47 generations. Individuals from generation 47 were sourced after one generation of common garden breeding (see Chapter 1). However, productivity in this generation was measured the same way as for the other generations, that is, identically to the way the individuals were reared in their selection lines (STP), or in a way that can be related to the way the individuals were reared in their selection lines (LTP; the difference being that lifetime offspring production, instead of offspring production during 48 hours, was measured, but otherwise similar in terms of cohabitation times and density conditions to the way selection lines were propagated). Therefore, all the productivity estimates in our assays can be interpreted as a proxy of population viability that is determined by the sum of

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genetic effects due to selection plus environmental effects due to differences in the inherent breeding conditions of the lines of each treatment. This is a relevant measure as population viability is a function of both genetic and environmental (including demographic) factors.

STP and LTP measures were based on the productivity of 400 females (n = 25 per each of the 16 selection lines within each experimental group) and 160 females (n = 10 per selection line), respectively, for each generation. However, since we could not track individually females in the polygamous experimental units (from NSPoly and Spoly lines), mean productivities per selection line were calculated and used in the analysis. The statistical sample size is therefore n = 16 per generation, for each of the productivity measures.

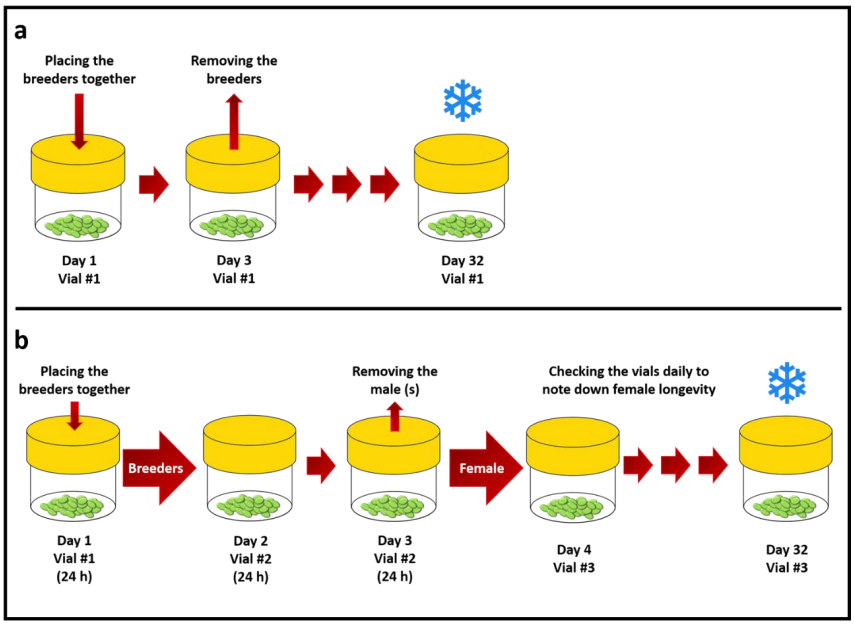

Fig. 4.1. The two complementary productivity measures that were assayed in the selection lines. (a) Short-term productivity (STP, female productivity within a 48-hours period). The breeders were placed together within a container with beans *ad libitum* where they remained for 48 hours. Twenty-nine days after the removal of the breeders, the containers with the newly emerged adult offspring were frozen for later counting. (b) Long-term productivity (LTP, female productivity along her lifetime). Breeders were placed together in a container with beans *ad libitum* for 24 hours (day 1), then transferred to a second vial (day 2) for 24 hours after which males were removed (day 3, 48 hours since the moment the breeders were housed together). Females were left in this container for 24 hours more, and then transferred (day 4) to the final third container with beans, where they remained the rest of their life. As for the STP measure, 29 days after the removal of the breeders the containers with the newly emerged adult offspring were frozen for counting at a later stage.

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Longevity

The analysis of female longevity focused on the data collected in generations 46 and 47. Female survival was checked daily in the LTP containers until all the females were found dead. The longevity of a total of 318 females (n = 159 per generation) was assessed. Generations 46 and 47 are analysed independently because in generation 47 individuals were sourced after common garden (but see note in the previous section about the fact that the assays in generation 47 are informative of traits determined by genetic effects due to selection plus environmental effects due to the breeding conditions of the lines within each treatment).

Body weight

In generation 47 males and females were weighed following the protocol described in Chapter 2 (Material and Methods section). Body weight was used as a covariate in the analyses run in this generation (see below). In this case, this trait, which was measured straightaway on the individuals after common garden breeding (i.e., without the influence of breeding conditions as they happen in the selection lines), can be interpreted as being mainly the result of genetic sources of variance.

Statistical analysis

All the analyses were carried out using R 3.3.2 (R Core Team 2016). The analyses of STP and LTP were carried out after square transforming these response variables, while female longevity was log-transformed before analysis. Both Linear Mixed Models (LMMs), and Generalized Linear Mixed models (GLMMs) with Poisson distribution, were fitted to the response variables using the functions '*lmer*' and '*glmer*', respectively, implemented within the package '*lme4*' (Bates et al. 2015). The traits assayed in this chapter are counts and therefore we analyzed them using GLMM with Poisson distribution. However, when the response of a count variable takes a very high number of values the variable can be treated as continuous variable (Zuur et al. 2009). In our case, both productivity and longevity presented a very high number of values (productivity across generations > 1300 categories; longevity > 10 categories), and for this reason we run confirmatory analyses on these variables using LMMs instead of GLMMs. Finally, additional GLMMs were run using the function '*glmmPQL*' from the package '*mass*' (Venables and Ripley 2002) to improve the dispersion of the residuals of the models using a quasipoisson distribution. In all cases both LMMs and GLMMs yielded the same results, and thus we show here only the results pertaining to LMMs.

The models included the following variables as predictors: generation, mating system selection treatment (monogamy/polygamy), population spatial structure selection treatment (metapopulation structure/no structure), and the interaction of these factors, as fixed factors, as well as the replicate line as a random factor nested within each combination of mating system and population spatial structure. Female longevity was included as a covariate in the analyses of LTP and, similarly, LTP variable was included in the models were female longevity was the response variable (with a same value of LTP per line, as LTP measures were estimated as a global measure per line, but female longevity was measured on the individual females). Furthermore, the models on LTP and female longevity at generation 47

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(following one generation of common garden) included mean male and female body weights per line as covariates. All the covariates were mean centered to improve the interpretability of regression coefficients, as recommended by Schielzeth (2010).

We were interested in the contribution of particular effects to variance in the dependent variables (i.e. hypothesis testing) rather than on finding the best model out of many competing ones. Thus, the focus of the analyses was to test the significance of effects. We followed the same protocol in all cases. First, we fitted the full model (the model with all the predictors and their interactions) and tested it against the null model (the model lacking the predictors of interest but including the random structure of the data, i.e., the random factor Selection Line) with a Likelihood Ratio Test (LRT) using the R function '*anova*' with argument test set to '*Chisq*'. It has been suggested that significance tests for individual predictors should only be considered once the full model reveals significance, unless an error-level adjustment for multiple testing is used to avoid inflation of Type-I error (Forstmeier and Schielzeth 2011). We adjusted *p* values for multiple testing using the Benjamini-Hochberg procedure (Benjamini and Hochberg 1995), to correct for such potential source of inflation of Type-I error.

We ran progressively simplified models by removing fixed effects (or their interactions) one-at-a-time using the '*drop1'* function (argument test set to '*Chi*') from the package '*stats*' (R Core Team 2016), and testing the effect of removal of each term on the change in model deviance using likelihood ratio tests and maximum likelihood (Bolker et al. 2009). The final model included the significant effects (alpha criterion of 0.05), and we also always retained in the final model the fixed factors mating system and population spatial structure plus the random factor Selection Line, regardless of the contribution of these factors, to account for the structure of the experimental design and the hierarchical structure of the data (i.e., for the fact that the data is grouped by the random factor within each combination of mating system and population structure selection levels). The LRT for the non-significant effects was calculated using the '*drop1'* function after adding the particular non-significant effect to the final model.

While significance of the fixed effects was calculated using maximum likelihood as described above, parameter estimates (coefficients, estimates) of the fixed and random effects in the final model were calculated using Restricted Maximum Likelihood (REML), as it has been suggested (Zuur et al. 2009). The random effect was tested with a likelihood ratio test (Lynch and Walsh 1998; Bolker et al. 2009), comparing the final model with the random term and using REML to the model without the random factor. The degrees of freedom of all the LRT and F-tests was always 1 because *drop1* compares two models (with and without the tested effect). Sample sizes have been indicated above (section 'Traits' of material and methods), and they have also been noted in the tables regarding the analysis of each response variable.

Pairwise comparisons among the levels within the explanatory fixed factors included in the models were done running post-hoc Tukey tests with the function '*lsmeans*' implemented in the package with the same name (Lenth 2016).

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The marginal (i.e., based on just the fixed effects) and conditional (i.e., including random effects) R^2 values for the final LMM model were calculated using the function '*sem.model.fits*' implemented in the package '*piecewiseSEM*' (Lefcheck 2016). We checked that the assumptions of the analysis (normality and homogeneity of residuals) were fulfilled by visually inspecting qqplots and plots of the distribution of the residuals against fitted values.

Due to the heterogeneity found in the results across generations (see Results section), we also run analyses for each generation separately. To this end, in the analyses of productivity we run linear models (LMs) using the function '*lm*' implemented in the R package '*stats*' (R Core Team 2016). We used LMs because our responses variables consisted in means calculated per selection line and there was therefore a single value for selection line and no need for the random factor selection line. To calculate the significance of the main effects as well as their interaction, the argument test of the *drop1* function was set to F in these models. The multiple (i.e., without correcting for the number of predictors) and adjusted (i.e., adjusting for the number of terms in the model) R^2 values for the final LM model were obtained using the function '*summary*' implemented in the R package '*base*' (R Core Team 2016).

The general protocol for the detection and removal of influential observations and outliers (see Chapter 2) was applied before carrying out the analysis of female longevity, but not in the analyses of productivity because the removal of any observation (line mean) in this dataset would have meant the removal of the information related to a whole selection line (experimental unit in experimental evolution settings). For the longevity data set, data from 9 females met the "influential outlier" criteria (n = 6 in generation 46 rendering a final sample size of 153 females analyzed, and n = 3 in generation 47, resulting in a final sample size for this generation of 156 females analyzed). We also run confirmatory analysis including all data to assess whether the inclusion of what we called 'influential outliers' rendered qualitatively different results to those from the main analysis. Results were identical before and after the removal of influential outliers and we just show here the results of the main analysis excluding influential outliers, because the data in this analysis provide a better fit to the assumptions of normality and homoscedasticity from linear models. We report mean ± standard error values throughout. Tables are provided after the references. Parameter estimates and other details of the models run can be found in the Appendix at the end of the chapter.

Results

Short-term productivity (STP)

The variation in STP responded to variation in the generation that productivity was measured (LRT = 7.91, df = 1, p = 0.0049, Fig. 4.2) (Table 4.1). In the analyses within generations, the results showed high consistency: neither the mating system, nor the spatial structure or their interaction had a significant effect on STP (see table 4.2). However, in generation 47, for which we used individuals generated after a generation of common garden (but measured their productivity as in the other generations, that is, mimicking the general conditions established in

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the selection lines; see Material and Methods), we detected a significant effect of variation in spatial structure on short-term productivity (F = 15.82, df = 1, p = 0.0016), with lines from spatially structured populations having lower short-term productivity than lines from non-structured populations (Fig. 4.3). Table 4.3 shows the STP means for each of the groups analyzed, both across and within generations and selection treatments.

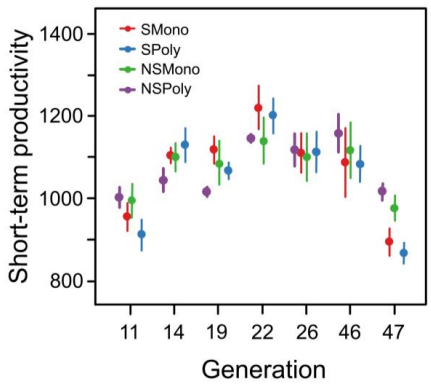
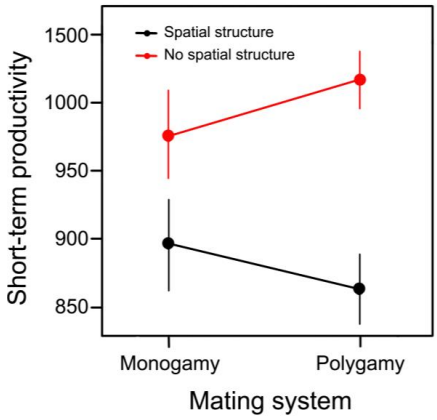


Fig. 4.2. Short-term productivity, STP in the four different selection regimes across generations. Mean values (and SE) for each selection line within each of the four selection regimes established (resulting from the combination of mating system and population spatial structure selection treatments) are shown.

Fig.4.3. The main and interactive effects of mating system (monogamy vs. polygamy) and spatial population structure (metapopulation structure vs. no structure) selection treatments on short-term productivity (STP) in generation 47. The graph depicts the mean (±1 SE) of the number of adults produced by the females in each selection regime (the result of the combination of the two selection treatments: SPoly, NSPoly, SMono, NSMono), calculated across the different lines (units of replication) for that particular selection regime. Data from populations with spatial structure are shown in black while data from populations without spatial structure are shown in red.



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Long-term productivity (LTP)

The main effects (mating system and population spatial structure selection treatments) or their interaction (see table 4.4) were not significant. However, as for STP, a significant effect of generation was observed on this productivity measure as well (LRT = 10.29, df = 1, p = 0.0013, Fig. 4.4). Additional analyses carried out within each generation separately, and also on data from generation 47, yielded similar results: mating system, population spatial structure or their interaction were not significant (see table 4.5). Likewise, the covariates female longevity (included within the analyses of each generation) and body weight (measured in generation 47) did not explain variation in LTP, though male body weight was marginally no significant (F= 4.41, p= 0.0575): females that mated with heavier males produced slightly higher numbers of offspring, regardless of the selection treatment under which they evolved (Fig. 4.5). Table 4.6 shows the LTP means for each of the groups analyzed, both across and within generations and selection treatments.

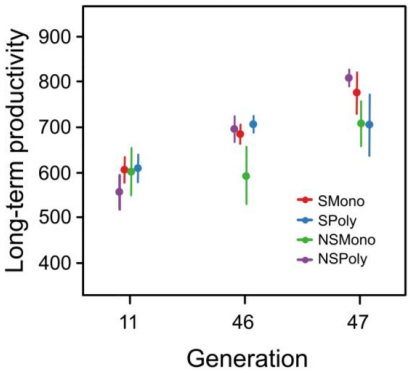
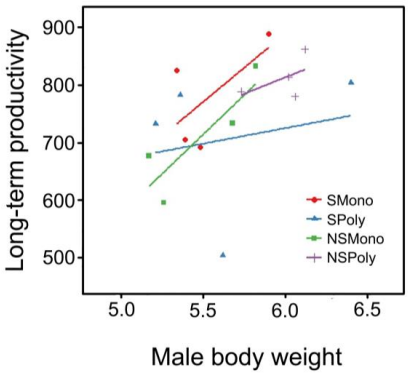


Fig. 4.4. Long-term productivity, LTP in the four different selection regimes across generations. Mean values (and SE) for each selection line within each of the four selection regimes established (resulting from the combination of mating system and population spatial structure selection treatments) are shown. Note that the lower values for LTP compared to STP (e.g., Fig 4.2) responds to the fact that LTP was measured using 10 females per line instead of 25 (see Material and Methods section).

Fig. 4.5. Relationship between male body weight (in milligrams) and long-term productivity in the selection lines. Mean values for each selection line within each of the four selection regimes established (resulting from the combination of mating system and population spatial structure selection treatments) are shown.



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Female longevity

Interestingly, a significant effect of mating system on female lifespan was detected after 46 generations of evolution (LRT = 17.6607, df = 1, p < 0.0001). Polygamous females had a shorter lifespan than monogamous ones (see Fig. 4.6a and table 4.7). The effect of population spatial structure was marginally no significant (LRT = 3.77, df = 1, p =0.0523), with females from structured populations living slightly longer than females from undivided populations. There were no significant interactive effects of the two selection regimes on female longevity (see table 4.7 and Fig. 4.6a). At generation 47, an interaction between mating system and spatial structure was detected, but after correcting for multiple testing the interaction was no longer significant (LRT = 5.49, df = 1, p = 0.019; Fig.4.6b). The interaction was due to the fact that the reduction in longevity that polygamous females exhibit compared to monogamous females in undivided populations is much more pronounced under spatial structure selection (Fig. 4.6b). Post hoc Tukey tests inform that the difference in female longevity between structured and non-structured populations is only significant when monogamous groups are compared (see table 4.8). Regardless of this interactive pattern, in generation 47, as in generation 46, it is clear that polyandrous females pay a cost in terms of longevity (Mating system LRT = 9.46, df = 1, p = 0.0021; Table 4.7 and Fig.4.6b). Finally, female body weight, but not male body weight, had a significant effect on female longevity (LRT = 4.94, df = 1, p = 0.026; see table 4.7) with heavier females living longer than lighter females (Fig. 4.7); however, this effect was no longer significant after the correction for multiple testing. Table 4.9 shows the means for female longevity for each of the groups analyzed.

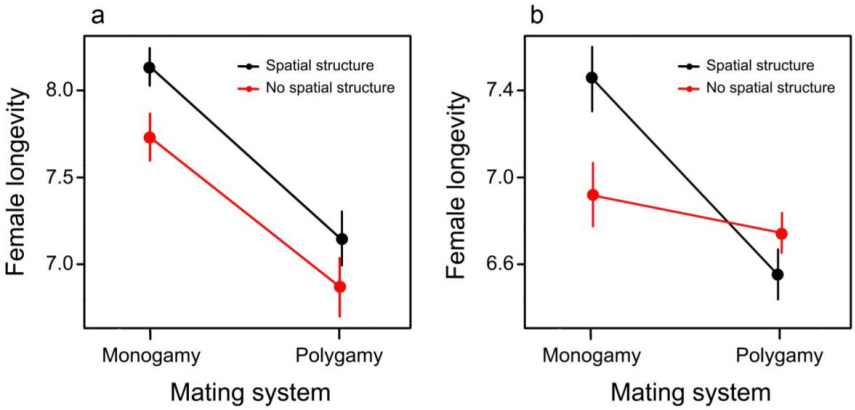

Fig. 4.6. The main and interactive effects of mating system (monogamy vs. polygamy) and spatial population structure (metapopulation structure vs. no structure) selection treatments on female longevity (in days) at generations 46 (a) and 47 (b). The image depicts the mean (±1SE) of the number of days that females were alive in each selection regime (the result of the combination of the two selection treatments: SPoly, NSPoly, SMono, NSMono), calculated across the different lines (units of replication) for that particular selection regime. Data from populations with spatial structure are shown in black while data from populations without spatial structure are shown in red.

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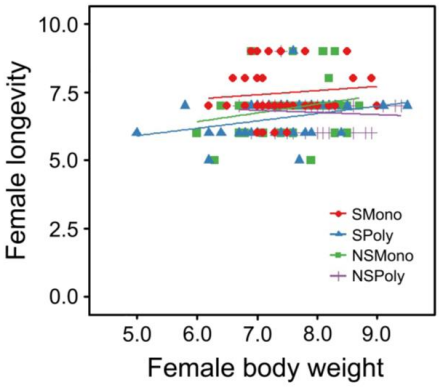

Fig. 4.7. Relationship between female body weight (in milligrams) and female longevity (in days) for each of the four selection regimes established (resulting from the combination of mating system and population spatial structure selection treatments).

Discussion

The question of whether (and how) sexual selection influences population viability and extinction rates is a hot topic in evolutionary biology. Determining the net effect of sexual selection upon population viability is challenging, and the scant research to date relating sexual selection to this population feature or to population extinction rates is inconclusive. Sexual selection has been proposed to slow down population extinction due the purging of deleterious alleles and the reduction of mutation loads (Hollis et al. 2009; Whitlock and Agrawal 2009; Jarzebowska and Radwan 2010; Almbro and Simmons 2014; Lumley et al. 2015; Grieshop et al. 2016; Singh et al. 2017), but not all studies support this contention (e.g Hollis and Houle 2011; Arbuthnott and Rundle 2012 and see Whitlock and Agrawal 2009). Likewise, polyandry has been showed to protect against extinction caused by selfish genetic elements (Price et al. 2010; Wade 2010), and some experimental studies have documented higher net reproductive rates for monogamous populations compared to polygamous populations (e.g. Holland and Rice 1999; Martin et al. 2004), but again, evidence is mixed (Martin and Hosken 2003; Godwin et al. 2017). In addition, sexual selection facilitates the accruement of direct and indirect benefits arising from mate choice and female multiple mating (Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Neff and Pitcher 2005; Simmons 2005; Kempenaers 2007; Garcia-Gonzalez et al. 2015) However, sexual selection often leads to sexual conflict and associated fitness costs (Parker 1979; Arnqvist and Rowe 2005; Rice and Gavrilets 2014). Arguably, sexual conflict complicates how sexual selection and population viability are connected (Whitlock and Agrawal 2009).

The relative moderate consideration, from an empirical perspective, that the study of the impact of sexual selection on population viability has received, is in sharp contrast to the very limited body of empirical research into the effects of a presumably important ecological and demographic feature such as population spatial structure on population viability. This is so despite it is widely accepted that population spatial structure has important implications for population

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dynamics and persistence (Sjögren 1991; Richards 2000; Haikola et al. 2001; Molofsky and Ferdy 2005; Muniz et al. 2017). It is, therefore paramount that both mating system and population spatial structure are taken into account, jointly if possible, and in both theoretical (see Yasui and Garcia-Gonzalez 2016) and empirical (here) research, when studying the causes underlying variation in population viability.

Our experimental evolution study using the seed beetle *Callosobruchus maculatus* addresses this gap of knowledge, by investigating the independent effects of variation in mating system (polygamy versus monogamy) and consequent influence of the presence/absence of sexual selection, and variation in population spatial structure (metapopulation structure versus no metapopulation structure), as well as their interactive effects, on proxies of population viability (short and long-term productivity, and female longevity). To the best of our knowledge, this is the first time that such an enquiry has been made.

In the analyses of short-term and long-term productivity, generation had a significant effect on productivity. However, the fluctuation across generations in productivity did not reflect a clear pattern, and we think that part of the variation across generations might be associated to slight differences in the size of the beans (oviposition substrate) among generations. In any case the analysis at the within-generation level, indicated that the lack of significant effects of the main factors included in the models, or their interaction, were consistent across generations. Mating system, spatial population structure or their interaction did not explain productivity in any of the generations, with the exception of spatial structure, which had a significant effect on STP in generation 47: productivity in spatially structured populations was lower than in non-structured populations.

It is unclear why STP is lower in structured populations. This result may suggest that sexual conflict is more intense under metapopulation structure, with females from subdivided populations (featuring smaller population sizes) incurring higher reproductive loads than females from undivided (larger) populations. However, this is against predictions from sexual conflict theory that sustain that the larger the population size the more intense sexual conflict is (Gavrilets 2000; Gay et al. 2009). Moreover, it is unclear why structured vs. undivided populations should differ in productivity also in contexts where sexual selection and sexual conflict is absent, that is, in our monogamous selection lines. Another relevant factor to be considered when assessing the potential outcomes of sexual conflict is the genetic relatedness of individuals as well as their familiarity. Recent research has shown that these two factors can modulate male harm to females based on the inclusive fitness payoffs that harming would have when males compete with relatives: higher relatedness and/or familiarity reduces male harm to females, leading to positive effects on female reproductive output and survival (Carazo et al. 2014; Pizzari et al. 2015; Le Page et al. 2017; Łukasiewicz et al. 2017; Lymbery and Simmons 2017) but also on male lifespan and fitness (Carazo et al. 2014; Pizzari et al. 2015). Such effects are indeed aligned with predictions stemming from kin selection and inclusive fitness ideas (Hamilton 1964). However, if anything, higher relatedness would be expected in our structured populations compared to non-structured populations, and so under the light of explanations based on genetic relatedness ameliorating sexual conflict we should have expected higher productivity in structured populations, when the reverse pattern was actually

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observed. In any case we are cautious drawing conclusions about variation in genetic relatedness among our lines, because we imposed moderate migration rates (20%) among subpopulations, which would have favoured gene flow to some extent. This very same reason speaks against differences in inbreeding underlying our results; while it would be reasonable to expect lower heterocigosity, higher inbreeding and higher accumulation of deleterious alleles in small (subdivided) populations (Bataillon and Kirkpatrick 2000; Richards 2000; Haikola et al. 2001; Hanski and Gaggiotti 2004; Hartl and Clark 2007), the moderate migration rates allowed in our experimental design would have presumably ameliorated potential differences in inbreeding among the selection lines. Moreover, additional results gathered in our selection experiment indicate that systematic differences in inbreeding among our populations are unlikely: e.g., there are no differences among our divided and undivided populations in regards to intrinsic mortality rates of the individuals (Chapter 5). Another potential explanation for the lower productivity in both monogamous and polygamous spatially structured populations compared to their undivided counterparts is the fact that mate sampling is more limited in small demes, and the detrimental consequences of mating with unsuitable partners (e.g., infertile males; see Garcia-Gonzalez 2004; Greenway et al. 2015; Yasui and Yoshimura 2018) are more pronounced in structured populations (Yasui and Garcia-Gonzalez 2016). Notwithstanding, future research is needed to discern the causes of differences in productivity between populations subjected to selection regimes varying in population spatial structure.

The analysis of the long-term productivity at generation 47 did not show any difference due to the structure, mating system or their interaction. This fact makes difficult to draw firm conclusions about the consequences of the selection treatments on population viability. Nevertheless, it should be noted that short-term productivity as we measured it reflects the real conditions under which our selection lines evolved and were propagated. The results relating to STP discussed above are therefore of higher relevance to assess the sources of variation in population viability in our selection lines.

Results in our study shows no effects of the removal of sexual selection on population's productivity (number of adult offspring produced to seed the next generations), regardless of the analysis (across- or within- generations). Previous studies have used experimental evolution to investigate the effect of monogamous and polygamous selection histories (i.e., absence and presence of sexual selection, respectively) on female fecundity and productivity (Holland and Rice 1999; Martin and Hosken 2003; Martin et al. 2004). In species with sexual conflict, including *C. maculatus*, data from experimental evolution, as well as comparative, studies, have shown that sexual selection in polygamous populations favours the evolution of harmful male traits that depress female fitness and that leads to higher populations costs in terms of productivity, compared to monogamous populations (e.g. Holland and Rice 1999; Blanckenhorn et al. 2002; Wigby and Chapman 2005; Hotzy and Arnqvist 2009). For instance, the classical study by Holland and Rice (1999) in *D. melanogaster* found a greater net reproductive rate for monogamous selection lines compared to polygamous populations. Similarly, Martin et al. (2004) found a relevant effect of mating system on productivity of the yellow dung fly *Scatophaga stercoraria*. These authors compared the longevity and lifetime reproductive success (analogous to our measure of long-term productivity) of

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females evolving under enforced monogamy and polygamy when females were mated only once with males from their same mating regime. Polygamous females had lower fitness and died earlier than their monogamous counterparts. Such difference was attributed to the costs implied by sexual conflict. However, as in our case, other studies have found no effect of the experimental manipulation of sexual selection history on population productivity or viability (Martin and Hosken 2003). In their study on the dung fly *Sepsis cynipsea*, Martin and Hosken (2003) compared the fitness of females evolving under polygamy or monogamy and found that despite polygamous females laid a higher number of eggs, there were no significant differences in terms of the LRS between the two mating tactics.

The reasons underlying a lack of effect of the presence of sexual selection on population productivity could be related to a balance between the costs of sexual conflict and the benefits of sexual selection. For females, the costs of sexual conflict can be compensated by direct (e.g., effects on fecundity) or indirect (e.g., genetic effects on egg-to-adult viability) accrued by multiple mating (Yasui 1998; Arnqvist and Nilsson 2000; Garcia-Gonzalez and Simmons 2005), or by mating with harmful but attractive and/or high quality males (e.g. Parker 1979; Cordero and Eberhard 2003; Garcia-Gonzalez and Simmons 2010). In many species, including species of the genus *Callosobruchus*, is known that ejaculate compounds such as seminal fluid proteins underlie direct effects on females (e.g. Chapman et al. 1995; Chapman and Davies 2004; Yamane and Miyatake 2010a, c; Avila et al. 2011; Xu and Wang 2011; Yamane 2013; Yamane et al. 2015). Female *C. maculatus* obtain benefits from the receipt of male ejaculates such as water and nutrients that boosts their fecundity, especially when females have no access to water or under starvation conditions (Fox 1993; Edvardsson 2007; Ursprung et al. 2009). A marginal non-significant effect of male body size on long-term productivity was detected in the experimental replicate carried out in generation 47, such that higher values of long-term productivity were positively correlated with larger male body sizes. This effect could be explained if larger males transferred larger volumes of ejaculate, as it is indeed the case in *C. maculatus* as well as in other seed beetles (Savalli and Fox 1998a, b). It is also known that in *C. maculatus* and related species larger amounts of seminal fluid proteins from the accessory glands modify female reproductive behavior, for example boosting egg-laying rates or reducing male mating receptivity (Yamane et al. 2008; Yamane and Miyatake 2010a, c, b). We cannot rule out, however, that such an effect of male body size on productivity was caused by differential female allocation, whereby females would allocate more resources to reproduction or to egg production when mating with larger males (Sheldon 2000). Finally, it is also possible that good genes may underlie the results, if larger males are of higher quality and if higher quality males sire higher quality offspring (e.g., offspring with higher egg-to-adult viability)(Møller and Alatalo 1999; Garcia-Gonzalez and Simmons 2005; Garcia-Gonzalez and Simmons 2011).

In contrast to the results of productivity the analysis of female longevity informed that selection under polygamous conditions entails a cost in terms of longevity. Specifically, polygamous females had shorter lifespans than monogamous females. This result, which was consistent across the two generations assayed, supports the predictions of sexual conflict theory whereby males would impose higher costs to females under polygamy than under monogamy, a result widely supported by

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previous research in other taxa (Holland and Rice 1999; Martin and Hosken 2003; Martin et al. 2004).

Differences in female longevity due to spatial structure were marginally no significant in generation 46, with females from structured populations living longer than females from non-structured populations. Taken together with the lower STP observed in structured populations compared to their undivided counterparts these results support the notion that there is a trade-off between early life fecundity/oviposition and longevity; evidence for this trade-off has emerged repeatedly along different experiments in this thesis (e.g., Chapter 5). Indeed, when female *C. maculatus* are not allowed to oviposit, their longevity is increased by a factor of three, on average (Rodriguez-Exposito and Garcia-Gonzalez, unpublished results). Such fecundity-longevity trade-offs, reflective of the existence of general costs of reproduction, is a well-known trade-off in life-history theory (Williams 1966; Kirkwood 1977; Reznick 1985; Stearns 1989; Stearns 1992; Brommer 2000; Edward and Chapman 2011). As for our particular species, results from other studies suggest that fecundity trades off against somatic maintenance, longevity or the investment in immune system (Fox 1993; Rönn et al. 2006; Dougherty et al. 2017 and see Messina and Fry 2003). For instance, Dougherty et al. (2017) documented a negative association between female immunity, a female resistance trait to male harm, and population productivity.

In generation 47 there was a trend for an interaction between mating system and spatial structure on female longevity. Females from structured populations lived longer than females from non-structured populations under monogamous selection, though in polygamous population such pattern was reversed. The results revealed that the difference between structured and non-structured populations was significant only under a monogamous mating system. These results point out towards interesting but complex combined effects of mating system and population spatial structure upon female longevity. Further analyses are warranted to shed light into the causes and mechanisms underlying this interaction.

Our results also show an influence of female body weight on female longevity in the analysis of generation 47 such that heavier females lived for longer. In general, individuals with larger body sizes are expected to live for longer (Calder III 1983; Fox and Czesak 2000). This is also the expectation in our experiment because under our laboratory conditions we did not supply food or water to the individuals once they emerged from the beans (nor they need it to complete the cycle), and therefore, they were forced to survive with the resources accrued during the larval stage. Thus, heavier females would have had more resources to invest in somatic maintenance and other biological functions, which would have ultimately determined their longevity.

In conclusion, we provide, for the first time, empirical evidence that selection stemming from variation in population spatial structure influences population productivity. In our study this effect was only apparent when short-term productivity was examined; it is important, however, to note that it is short-term productivity the productivity under selection in our experimental evolution protocol, and thus the most relevant measure in our study to investigate the links between the selection regimes and population viability. On the other hand, the

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presence or absence of sexual selection alone seems not to influence productivity to a large extent, even when our results show that the manipulation of sexual selection clearly affects female longevity as predicted by sexual conflict theory. Our study provides important novel insights into the effects of mating system and population spatial structure selection histories, on their own or in combination, on female longevity and population productivity, and will hopefully spur future theoretical and empirical research to improve our understanding of the relevant factors that ultimately determine the viability and probability of extinction of populations.

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Table 4.1. Analysis of short-term productivity across generations 11, 14, 19, 22, 26 and 46. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal R^2= 0.08; conditional R^2= 0.12.

Generation	Effect	LRT	p
11 to 46	**Mating system : structure**	0.04	0.84
	Mating system	0.35	0.56
	Structure	0.04	0.84
	Generation	7.91	**0.0049**
	Line (Random)	0.32	0.57

Table 4.2. Analysis of short-term productivity per generation. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text).

Generation	Effect	F	p
11	**Mating system : structure**	0.61	0.45
	Mating system	0.32	0.58
	Structure	3.68	0.08
14	**Mating system : structure**	1.39	0.26
	Mating system	0.24	0.64
	Structure	1.81	0.20
19	**Mating system : structure**	0.06	0.82
	Mating system	3.31	0.09
	Structure	1.44	0.25
22	**Mating system : structure**	0.08	0.78
	Mating system	0.04	0.85
	Structure	2.22	0.16
26	**Mating system : structure**	0.03	0.86
	Mating system	0.03	0.87
	Structure	0.0001	0.99
46	**Mating system : structure**	0.15	0.70
	Mating system	0.08	0.78
	Structure	0.80	0.39
47	**Mating system : structure**	1.58	0.23
	Mating system	0.02	0.89
	Structure	15.82	**0.0016**

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Table 4.3. Means ± 1 SE and sample sizes (within brackets) for the measures of STP (short-term productivity) for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). Sample size refers to the number of replicated selection lines within each group.

Generation	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Generations 11-46 combined	1099.88 ± 24.22 (24)	1082.0 ± 23.67 (24)	1090.63± 21.78 (24)	1081.96± 17.08 (24)	1095.25 ± 16.13 (48)	1087.98 ± 14.44 (48)	1090.94 ± 16.80 (48)	1086.29 ± 13.71 (48)
11	956.5 ± 34.24 (4)	909.0 ± 38.02 (4)	996.0 ± 42.06 (4)	1004.0 ± 26.06 (4)	976.25 ± 26.19 (8)	956.50 ± 27.88 (8)	932.75 ± 25.33 (8)	1000.00 ± 22.95 (8)
14	1105.75 ± 19.59 (4)	1128.25 ± 41.93 (4)	1099.75 ± 35.69 (4)	1045.0 ± 29.43 (4)	1102.75 ± 18.88 (8)	1086.63 ± 28.46 (8)	1117.0 ± 21.84 (8)	1072.38 ± 23.79 (8)
19	1117.50 ± 34.91 (4)	1065.00 ± 21.02 (4)	1085.75 ± 55.10 (4)	1016.75 ± 10.26 (4)	1101.63 ± 30.79 (8)	1040.88 ± 14.16 (8)	1091.25 ± 21.31 (8)	1051.25 ± 29.04 (8)
22	1220.75 ± 53.71 (4)	1199.25 ± 43.45 (4)	1143.00 ± 56.87 (4)	1147.50 ± 11.15 (4)	1181.88 ± 39.08 (8)	1173.38 ± 22.95 (8)	1210.00 ± 32.24 (8)	1145.25 ± 26.84 (8)
26	1110.50 ± 49.06 (4)	1109.75 ± 51.01 (4)	1101.00 ± 59.60 (4)	1118.50 ± 41.45 (4)	1105.75 ± 35.78 (8)	1114.13 ± 30.47 (8)	1110.13 ± 32.76 (8)	1109.750 ± 33.77 (8)
46	1088.25 ± 83.67 (4)	1080.75 ± 44.98 (4)	1118.25 ± 68.79 (4)	1160.00 ± 46.01 (4)	1103.25 ± 50.46 (8)	1120.38 ± 33.34 (8)	1084.50 ± 43.99 (8)	1139.13 ± 39.12 (8)
47	895.75 ± 33.86 (4)	863.50 ± 25.89 (4)	976.75 ± 32.74 (4)	1017.00 ± 20.94 (4)	936.25 ± 26.64 (8)	940.25 ± 32.85 (8)	879.63 ± 20.65 (8)	996.88 ± 19.53 (8)

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Table 4.4. Analysis of long-term productivity at generations 11 and 46. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal R^2= 0.2878; conditional R^2= 0.536.

Generation	Effect	F	p
11-46	**Mating system : structure**	0.07	0.79
	Mating system	0.50	0.48
	structure	1.66	0.19
	Female longevity	0.12	0.73
	generation	10.29	**0.0013**
	Line (Random)	2.18	0.14

Table 4.5. Analysis of long-term productivity per generation. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text).

Generation	Effect	F	p
11	**Mating system : structure**	0.39	0.54
	Mating system	0.28	0.61
	Structure	0.54	0.47
	Female longevity	1.24	0.29
46	**Mating system : structure**	1.14	0.31
	Mating system	2.68	0.13
	Structure	1.74	0.21
	Female longevity	1.04	0.33
47	**Mating system : structure**	1.63	0.23
	Mating system	0.42	0.53
	structure	0.0082	0.93
	Female longevity	1.56	0.24
	Male body weight	4.41	0.058
	Female body weight	1.39	0.26

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Table 4.6. Means ± 1 SE and sample sizes (within brackets) for the measures of LTP (long-term productivity) for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). Sample size refers to the number of replicated selection lines per group.

Generation	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Generations 11 and 46 combined	644.88 ± 22.49 (8)	658.13 ± 25.29 (8)	597.50 ± 38.49 (8)	626.75 ± 34.89 (8)	621.19 ± 22.39 (16)	642.44 ± 21.21 (16)	651.50 ± 16.44 (16)	612.13 ± 25.38 (16)
11	604.75 ± 28.07 (4)	609.25 ± 31.78 (4)	601.25 ± 53.18 (4)	556.25 ± 39.05 (4)	603.00 ± 27.84 (8)	582.75 ± 25.37 (8)	607.00 ± 19.64 (8)	578.75 ± 31.70 (8)
46	685.00 ± 22.39 (4)	707.00 ± 19.56 (4)	593.75 ± 63.84 (4)	697.25 ± 29.05 (4)	639.38 ± 35.75 (8)	702.13 ± 16.32 (8)	696.00 ± 14.38 (8)	645.50 ± 37.90 (8)
47	775.75 ± 47.334 (4)	704.25 ± 68.72 (4)	708.00 ± 49.82 (4)	809.25 ± 18.38 (4)	741.88 ± 34.29 (8)	756.75 ± 38.44 (8)	740.00 ± 40.92 (8)	758.63 ± 31.15 (8)

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Table 4.7. Analysis of female longevity per generation. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: generation 46 (marginal R^2= 0.2457; conditional R^2= 0.28), generation 47 (marginal R^2= 0.1774; conditional R^2= 0.1876).

Generation	Effect	LRT	p
46	**Mating system : structure**	0.05	0.82
	Mating system	17.66	**<0.0001**
	Structure	3.77	0.0522
	Long-term productivity	0.18	0.67
	Line (Random)	1.17	0.28
47	**Mating system : structure**	5.49	0.0191
	Mating system	9.46	**0.0021**
	Structure	2.06	0.1516
	Long-term productivity	1.61	0.21
	Male body weight	0.17	0.68
	Female body weight	4.94	0.0261
	Line (Random)	0.10	0.76

Table 4.8. Tukey tests pairwise comparisons of female longevity in the selection regimes resulting from the interaction of mating and population spatial structure at generation 47. The degrees of freedom were calculated with Satterthwaite's method.

Contrast	Estimate	SE	df	t-ratio	p
SMono- SPoly	0.11	0.02	16.04	4.82	0.001
SMono- NSMono	0.07	0.02	15.83	3.04	0.04
SMono- NSPoly	0.09	0.02	16.97	4.15	0.003
SPoly - NSMono	-0.04	0.02	16.19	-1.78	0.32
SPoly - NSPoly	-0.01	0.02	17.30	0.56	0.94
NSMono- NSPoly	0.03	0.02	16.12	1.20	0.64

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Table 4.9. Means ± 1 SE and sample size (within brackets) of female longevity within each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). Sample size refers to the number of replicate lines and the total number of females respectively, per group.

Generation	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
46	8.13 ± 0.11 (4; 38)	7.15 ± 0.15 (4; 40)	7.73 ± 0.14 (4; 37)	6.87 ± 0.17 (4; 38)	7.93 ± 0.09 (8; 75)	7.013 ± 0.11 (8; 78)	7.63 ± 0.11 (8; 78)	7.29 ± 0.12 (8; 75)
47	7.46 ± 0.15 (4; 39)	6.55 ± 0.12 (4; 38)	6.92 ± 0.15 (4; 39)	6.75 ± 0.09 (4; 40)	7.19 ± 0.1095 (8; 78)	6.65 ± 0.07 (8; 78)	7.01 ± 0.11 (8; 77)	6.84 ± 0.09 (8; 79)

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Appendix Chapter 4

Model: Evolution of short-term productivity across generations

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations todegrees of
freedom [lmerMod]. Formula: prod1 ~ ss +structure+ss:structure+gen+ (1|line)
   Data: datasinCG
     AIC      BIC   logLik deviance df.resid
  1171.8   1189.7   -578.9   1157.8       89
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.34877 -0.64313 -0.02568  0.66231  2.34363
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)  382.4   19.56
 Residual             9772.7   98.86
Number of obs: 96, groups:  line, 16
Fixed effects:
                        Estimate Std. Error        df t value Pr(>|t|)
(Intercept)            1041.1900    30.2829   46.8700  34.382  < 2e-16 ***
sspoly                  -17.8750    31.7114   16.0000  -0.564  0.58079
structurenometa          -9.2500    31.7114   16.0000  -0.292  0.77427
gen                       2.5515     0.8849   80.1000   2.883  0.00505 **
sspoly:structurenometa    9.2083    44.8467   16.0000   0.205  0.83990
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: prod1 ~ ss + structure + gen + (1 | line)
   Data: datasinCG
     AIC      BIC   logLik deviance df.resid
  1169.8   1185.2   -578.9   1157.8       90
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.32856 -0.64550 -0.02629  0.68034  2.32439
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)  387.7   19.69
 Residual             9772.7   98.86
Number of obs: 96, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)     1038.8879    28.1486   56.6500  36.907  < 2e-16 ***
sspoly           -13.2708    22.4529   16.0000  -0.591  0.56274
structurenometa   -4.6458    22.4529   16.0000  -0.207  0.83869
gen                2.5515     0.8849   79.9400   2.883  0.00505 **
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Evolution of short-term productivity per generation

Generation 11

Full model

```
lm(formula = prod1 ~ ss + structure + ss:structure, data = datasinCG11)
Residuals:
   Min     1Q Median     3Q    Max
-93.00 -52.88  -7.50  54.75 111.00
Coefficients:
                       Estimate Std. Error t value Pr(>|t|)
(Intercept)              956.50      35.59  26.877 4.32e-12 ***
```


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```
sspoly                   -47.50      50.33  -0.944    0.364
structurenometa           39.50      50.33   0.785    0.448
sspoly:structurenometa    55.50      71.18   0.780    0.451
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 71.18 on 12 degrees of freedom
Multiple R-squared:  0.2722, Adjusted R-squared:  0.09019
F-statistic: 1.496 on 3 and 12 DF,  p-value: 0.2657
```

Minimal model

```
lm(formula = prod1 ~ ss + structure, data = datasinCG11)
Residuals:
    Min      1Q  Median      3Q     Max
-106.88  -39.00  -17.88   68.62   97.12
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)       942.62      30.35  31.057 1.39e-13 ***
sspoly            -19.75      35.05  -0.564   0.5827
structurenometa    67.25      35.05   1.919   0.0772 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 70.09 on 13 degrees of freedom
Multiple R-squared:  0.2353, Adjusted R-squared:  0.1176
F-statistic:     2 on 2 and 13 DF,  p-value: 0.1749
```

Generation 14

Full model

```
lm(formula = prod1 ~ ss + structure + ss:structure, data = datasinCG14)
Residuals:
    Min      1Q  Median      3Q     Max
-107.25  -45.00   -5.50   36.38   94.25
Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)             1105.75      32.72  33.794 2.86e-13 ***
sspoly                    22.50      46.27   0.486    0.636
structurenometa           -6.00      46.27  -0.130    0.899
sspoly:structurenometa   -77.25      65.44  -1.180    0.261
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 65.44 on 12 degrees of freedom
Multiple R-squared:  0.2256, Adjusted R-squared:  0.03203
F-statistic: 1.165 on 3 and 12 DF,  p-value: 0.3634
```

Minimal model

```
lm(formula = prod1 ~ ss + structure, data = datasinCG14)
Residuals:
    Min      1Q  Median      3Q     Max
-87.938 -44.562  -9.688  39.187 113.562
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)      1125.06      28.76  39.116 7.15e-15 ***
sspoly            -16.12      33.21  -0.486    0.635
structurenometa   -44.62      33.21  -1.344    0.202
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 66.42 on 13 degrees of freedom
Multiple R-squared:  0.1357, Adjusted R-squared:  0.002733
F-statistic: 1.021 on 2 and 13 DF,  p-value: 0.3875
```


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Generation 19

Full model

```
lm(formula = prod1 ~ ss + structure + ss:structure, data = datasinCG19)
Residuals:
     Min       1Q   Median       3Q      Max
-140.750  -21.187    7.125   17.688  128.250
Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)            1117.50      34.65  32.252 4.99e-13 ***
sspoly                  -52.50      49.00  -1.071    0.305
structurenometa         -31.75      49.00  -0.648    0.529
sspoly:structurenometa  -16.50      69.30  -0.238    0.816
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 69.3 on 12 degrees of freedom
Multiple R-squared:  0.2711, Adjusted R-squared:  0.08889
F-statistic: 1.488 on 3 and 12 DF,  p-value: 0.2676
```

Minimal model

```
lm(formula = prod1 ~ ss + structure, data = datasinCG19)
Residuals:
     Min       1Q   Median       3Q      Max
-136.625  -25.312    9.125   18.063  132.375
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)      1121.62      28.90  38.814  7.9e-15 ***
sspoly            -60.75      33.37  -1.821   0.0918 .
structurenometa   -40.00      33.37  -1.199   0.2520
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 66.74 on 13 degrees of freedom
Multiple R-squared:  0.2677, Adjusted R-squared:  0.155
F-statistic: 2.376 on 2 and 13 DF,  p-value: 0.132
```

Generation 22

Full model

```
lm(formula = prod1 ~ ss + structure + ss:structure, data = datasinCG22)
Residuals:
    Min      1Q  Median      3Q     Max
-146.75  -30.94   -4.00   42.19  138.00
Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)            1220.75      45.09  27.075 3.97e-12 ***
sspoly                  -21.50      63.76  -0.337    0.742
structurenometa         -77.75      63.76  -1.219    0.246
sspoly:structurenometa   26.00      90.18   0.288    0.778
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 90.18 on 12 degrees of freedom
Multiple R-squared:  0.1538, Adjusted R-squared:  -0.05776
F-statistic: 0.727 on 3 and 12 DF,  p-value: 0.5553
```

Minimal model

```
lm(formula = prod1 ~ ss + structure, data = datasinCG22)
Residuals:
    Min      1Q  Median      3Q     Max
-144.50  -34.81    2.50   48.69  131.50
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)      1214.25      37.65  32.255 8.57e-14 ***
```


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```
sspoly             -8.50      43.47  -0.196    0.848
structurenometa   -64.75      43.47  -1.490    0.160
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 86.94 on 13 degrees of freedom
Multiple R-squared:  0.1479, Adjusted R-squared:  0.01685
F-statistic: 1.129 on 2 and 13 DF,  p-value: 0.3532
```

Generation 26

Full model

```
lm(formula = prod1 ~ ss + structure + ss:structure, data = datasinCG26)
Residuals:
    Min      1Q  Median      3Q     Max
-142.75  -74.88   15.88   83.44  112.50
Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)            1110.50      50.69  21.906 4.81e-11 ***
sspoly                   -0.75      71.69  -0.010    0.992
structurenometa          -9.50      71.69  -0.133    0.897
sspoly:structurenometa   18.25     101.39   0.180    0.860
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 101.4 on 12 degrees of freedom
Multiple R-squared:  0.004955,        Adjusted R-squared:  -0.2438
F-statistic: 0.01992 on 3 and 12 DF,  p-value: 0.996
```

Minimal model

```
lm(formula = prod1 ~ ss + structure, data = datasinCG26)
Residuals:
    Min      1Q  Median      3Q     Max
-147.31  -72.19   15.88   78.88  117.06
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)     1105.938     42.236  26.185 1.24e-12 ***
sspoly             8.375     48.770   0.172    0.866
structurenometa   -0.375     48.770  -0.008    0.994
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 97.54 on 13 degrees of freedom
Multiple R-squared:  0.002268,        Adjusted R-squared:  -0.1512
F-statistic: 0.01477 on 2 and 13 DF,  p-value: 0.9854
```

Generation 46

Full model

```
lm(formula = prod1 ~ ss + structure + ss:structure, data = datasinCG46)
Residuals:
    Min      1Q  Median      3Q     Max
-174.25  -76.44  -26.88  120.19  191.75
Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)            1088.25      63.00  17.275 7.66e-10 ***
sspoly                   -7.50      89.09  -0.084    0.934
structurenometa          30.00      89.09   0.337    0.742
sspoly:structurenometa   49.25     125.99   0.391    0.703
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 126 on 12 degrees of freedom
Multiple R-squared:  0.0754, Adjusted R-squared:  -0.1558
F-statistic: 0.3262 on 3 and 12 DF,  p-value: 0.8065
```

Minimal model

```
lm(formula = prod1 ~ ss + structure, data = datasinCG46)
```


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```
Residuals:
    Min      1Q  Median      3Q     Max
-161.94  -73.41  -26.12  114.03  179.44
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)      1075.94      52.75  20.397 2.96e-11 ***
sspoly             17.12      60.91   0.281    0.783
structurenometa    54.62      60.91   0.897    0.386
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 121.8 on 13 degrees of freedom
Multiple R-squared:  0.06363,	Adjusted R-squared:  -0.08043
F-statistic: 0.4417 on 2 and 13 DF,  p-value: 0.6523
```

Generation 47

Full model

```
lm(formula = prod1 ~ ss + structure + ss:structure, data = dataCG)
Residuals:
    Min      1Q  Median      3Q     Max
-97.750 -36.125   4.625  33.000  92.250
Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)             895.75      28.84  31.061  7.8e-13 ***
sspoly                  -32.25      40.78  -0.791   0.4444
structurenometa          81.00      40.78   1.986   0.0703 .
sspoly:structurenometa   72.50      57.68   1.257   0.2327
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 57.68 on 12 degrees of freedom
Multiple R-squared:  0.6017, Adjusted R-squared:  0.5022
F-statistic: 6.043 on 3 and 12 DF,  p-value: 0.009492
```

Minimal model

```
lm(formula = prod1 ~ ss + structure, data = dataCG)
Residuals:
    Min      1Q  Median      3Q     Max
-115.88  -26.06    5.25   24.38  110.38
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)       877.62      25.53  34.382 3.77e-14 ***
sspoly              4.00      29.47   0.136  0.89413
structurenometa   117.25      29.47   3.978  0.00158 **
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 58.95 on 13 degrees of freedom
Multiple R-squared:  0.5493, Adjusted R-squared:  0.4799
F-statistic: 7.922 on 2 and 13 DF,  p-value: 0.005628
```

Model: Evolution of long-term productivity across generations

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: prod2 ~ ss+structure+ss:structure+gen+centlongev+(1|line)
     AIC      BIC   logLik deviance df.resid
   378.4    390.1   -181.2    362.4       24
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.5824 -0.5078  0.1787  0.4110  1.9680
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 1795     42.36
 Residual             3381     58.14
```


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```
Number of obs: 32, groups:  line, 16
Fixed effects:
                      Estimate Std. Error      df t value Pr(>|t|)
(Intercept)            617.686     45.929  32.000  13.449 1.02e-14 ***
sspoly                  19.433     45.346  20.450   0.429    0.673
structurenometa        -43.541     43.164  17.680  -1.009    0.327
gen46                   44.608     97.487  21.520   0.458    0.652
centlongev               9.894     28.340  21.820   0.349    0.730
sspoly:structurenometa  15.505     59.051  15.860   0.263    0.796
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: prod2 ~ ss + structure + gen + (1 | line)
     AIC      BIC   logLik deviance df.resid
   374.6    383.4   -181.3    362.6       26
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.6875 -0.5050  0.1339  0.3928  1.8950
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 1867     43.21
 Residual             3361     57.98
Number of obs: 32, groups:  line, 16
Fixed effects:
                Estimate Std. Error     df t value Pr(>|t|)
(Intercept)       601.94      27.75  20.93  21.689 8.88e-16 ***
sspoly             21.25      29.78  16.00   0.714  0.48579
structurenometa   -39.38      29.78  16.00  -1.322  0.20471
gen46              77.87      20.50  16.00   3.799  0.00157 **
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Evolution of long-term productivity per generation

Generation 11

Full model

```
lm(formula = prod2 ~ ss + structure + ss:structure + centlongev, data = datag11)
Residuals:
    Min      1Q  Median      3Q     Max
-112.47  -47.83  -13.48   49.76  146.53
Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)             788.34     207.67   3.796  0.00296 **
sspoly                   16.20      57.39   0.282  0.78293
structurenometa          -3.50      55.90  -0.063  0.95120
centlongev              117.03     129.96   0.900  0.38715
sspoly:structurenometa  -20.24      85.47  -0.237  0.81712
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 79.05 on 11 degrees of freedom
Multiple R-squared:  0.1523, Adjusted R-squared:  -0.156
F-statistic: 0.4941 on 4 and 11 DF,  p-value: 0.7406
```

Minimal model

```
lm(formula = prod2 ~ ss + structure, data = datag11)
Residuals:
     Min       1Q   Median       3Q      Max
-108.875  -58.000    4.125   49.875  150.125
```


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```
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)       617.12      33.16  18.608 9.42e-11 ***
sspoly            -20.25      38.29  -0.529    0.606
structurenometa   -28.25      38.29  -0.738    0.474
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 76.59 on 13 degrees of freedom
Multiple R-squared:  0.05959,	Adjusted R-squared:  -0.08508
F-statistic: 0.4119 on 2 and 13 DF,  p-value: 0.6707
```

Generation 46

Full model

```
lm(formula = prod2 ~ ss + structure + ss:structure + centlongev, data = datag46)
Residuals:
     Min       1Q   Median       3Q      Max
-137.135  -42.938    2.357   47.242  112.975
Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)             589.49     124.14   4.749 0.000601 ***
sspoly                   64.97      76.18   0.853 0.411978
structurenometa         -62.29      65.32  -0.954 0.360718
centlongev               37.36      46.15   0.810 0.435356
sspoly:structurenometa   68.42      78.96   0.867 0.404712
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 77.29 on 11 degrees of freedom
Multiple R-squared:  0.3571, Adjusted R-squared:  0.1234
F-statistic: 1.528 on 4 and 11 DF,  p-value: 0.261
```

Minimal model

```
lm(formula = prod2 ~ ss + structure, data = datag46)
Residuals:
     Min       1Q   Median       3Q      Max
-177.125  -39.688    6.125   43.313  102.875
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)       664.62      33.17  20.038 3.71e-11 ***
sspoly             62.75      38.30   1.638    0.125
structurenometa   -50.50      38.30  -1.319    0.210
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 76.6 on 13 degrees of freedom
Multiple R-squared:  0.2539, Adjusted R-squared:  0.1391
F-statistic: 2.211 on 2 and 13 DF,  p-value: 0.1491
```

Generation 47

Full model

```
lm(formula = prod2 ~ ss + structure + ss:structure + centlongev + centmbw + centfbw, data = data)
Residuals:
     Min       1Q   Median       3Q      Max
-166.851  -35.308    7.506   64.358  120.453
Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)             771.44      76.15  10.131 3.21e-06 ***
sspoly                  -43.28     124.95  -0.346    0.737
structurenometa         -43.46      82.07  -0.530    0.609
centlongev               23.82      97.70   0.244    0.813
centmbw               99432.11   90744.67   1.096    0.302
centfbw               42164.39   71149.21   0.593    0.568
sspoly:structurenometa   84.99     123.13   0.690    0.507
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```


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```
Residual standard error: 98.13 on 9 degrees of freedom
Multiple R-squared:  0.4204, Adjusted R-squared:  0.03396
F-statistic: 1.088 on 6 and 9 DF,  p-value: 0.4364
```

Minimal model

```
lm(formula = prod2 ~ ss + structure, data = data)
Residuals:
    Min      1Q  Median      3Q     Max
-244.44  -32.06   16.44   60.88  153.44
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)       732.56      46.08   15.90 6.73e-10 ***
sspoly             14.88      53.21    0.28    0.784
structurenometa    18.62      53.21    0.35    0.732
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 106.4 on 13 degrees of freedom
Multiple R-squared:  0.0152, Adjusted R-squared:  -0.1363
F-statistic: 0.1003 on 2 and 13 DF,  p-value: 0.9052
```

Model: Evolution of female longevity per generation

Generation 46

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llongev ~ ss + structure + ss:structure + centprod2 + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -240.4   -219.2    127.2   -254.4      146
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.7567 -0.7617  0.0246  0.4490  3.2757
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0004715 0.02172
 Residual             0.0106985 0.10343
Number of obs: 153, groups:  line, 16
Fixed effects:
                        Estimate Std. Error         df t value Pr(>|t|)
(Intercept)             2.210e+00  2.013e-02  1.665e+01 109.786  < 2e-16 ***
sspoly                 -1.162e-01  2.821e-02  1.598e+01  -4.119 0.000806 ***
structurenometa        -5.282e-02  3.125e-02  1.612e+01  -1.690 0.110259
centprod2              -8.086e-05  1.567e-04  1.867e+01  -0.516 0.612014
sspoly:structurenometa  1.533e-02  4.164e-02  1.622e+01   0.368 0.717471
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llongev ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -244.1   -229.0    127.1   -254.1      148
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.7821 -0.8401 -0.0003  0.3982  3.2499
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000509 0.02256
 Residual             0.010694 0.10341
Number of obs: 153, groups:  line, 16
```


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```
Fixed effects:
                Estimate Std. Error       df t value Pr(>|t|)
(Intercept)      2.20653    0.01750 16.60900 126.054  < 2e-16 ***
sspoly          -0.11335    0.02019 16.47600  -5.614 3.48e-05 ***
structurenometa -0.04146    0.02019 16.47600  -2.053   0.0563 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Generation 47

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llongev ~ ss + structure + ss:structure + centprod2 + centmbw + centfbw
+ (1 | line)
     AIC      BIC   logLik deviance df.resid
  -268.9   -241.5    143.5   -286.9      147
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.9239 -0.7149  0.1185  0.4441  2.9022
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 4.316e-05 0.00657
 Residual             9.264e-03 0.09625
Number of obs: 156, groups:  line, 16
Fixed effects:
                        Estimate Std. Error         df t value Pr(>|t|)
(Intercept)             2.131e+00  1.631e-02  1.689e+01 130.659  < 2e-16 ***
sspoly                 -1.041e-01  2.351e-02  1.640e+01  -4.429 0.000398 ***
structurenometa        -6.173e-02  2.341e-02  1.636e+01  -2.637 0.017700 *
centprod2               1.239e-04  1.003e-04  2.065e+01   1.236 0.230497
centmbw                 2.549e+00  1.452e+01  1.360e+02   0.175 0.860957
centfbw                 2.015e+01  1.190e+01  1.452e+02   1.693 0.092519 .
sspoly:structurenometa  6.462e-02  3.509e-02  1.547e+01   1.841 0.084845 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llongev ~ ss + structure + ss:structure + centfbw + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -271.3   -249.9    142.6   -285.3      149
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.9003 -0.6345  0.1068  0.4283  2.8684
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0001163 0.01078
 Residual             0.0092942 0.09641
Number of obs: 156, groups:  line, 16
Fixed effects:
                        Estimate Std. Error        df t value Pr(>|t|)
(Intercept)              2.13450    0.01649  16.07000 129.428  < 2e-16 ***
sspoly                  -0.11201    0.02326  16.04000  -4.815 0.000189 ***
structurenometa         -0.07059    0.02320  15.83000  -3.043 0.007822 **
centfbw                 25.36658   11.18678 114.80000   2.268 0.025228 *
sspoly:structurenometa   0.08391    0.03302  16.07000   2.541 0.021731 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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Chapter 5

The evolution of sexual conflict adaptations including male harm and female resistance in response to variation in sexual selection and population spatial structure: an experimental evolution approach with *Callosobruchus maculatus*

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The evolution of sexual conflict adaptations including male harm and female resistance in response to variation in sexual selection and population spatial structure: an experimental evolution approach in *Callosobruchus maculatus*.

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Abstract

Sexual conflict is now recognized as an important force underlying fundamental evolutionary processes. However, several critical questions have been largely neglected in the study of sexually antagonistic selection. One such question relates to the role of population subdivision on the dynamics of sexual conflict. Here we use experimental evolution in the seed beetle *Callosobruchus maculatus* to assess the independent and interacting effects of selection associated to mating system and population spatial structure on a series of adaptations to sexual conflict in both sexes. We measured evolutionary responses in several behavioural traits expressed during mating interactions. We also assessed the evolution of male harm and female resistance by gauging the outcomes of mating interactions on female longevity and lifetime reproductive success. The lack of clear effects derived from sexual selection for the majority of traits assayed in our study suggests that sexual conflict in this species may not be as intense as previously thought. Population spatial structure, however, influenced traits related to the control of copulation duration, including female kicking behaviour. We also detected an interaction between sexual selection and population spatial structure selection treatments on female productivity and longevity, when females were continuously exposed to males. Body size in general significantly affected most of the traits assayed, stressing the relevance of this phenotypic trait for sexual selection and sexual conflict. Our results also support the existence of trade-offs between different biological functions, such as somatic maintenance and reproduction, as predicted by life-history theory. Finally, variation in the direction of the relationship between female lifetime reproductive success and female longevity, which depended on whether sexual interactions were punctual or sustained along time indicates that the evolution of key trade-offs between life-history traits in sexual conflict systems depends on a complex and delicate balance between the benefits and costs of sexual interactions (including those associated to multiple mating for example).

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Introduction

Males and females have different evolutionary interests when it comes to reproduction. This sexual conflict (Parker 1979) shapes many aspects of reproduction and mating interactions, including courtship, mating, fertilization and parental care (Arnqvist and Rowe 2005; Chapman 2006; Firman et al. 2014; McNamara and Wolf 2015). Reproduction implies different costs for males and females due to basic asymmetries between sexes regarding gamete production and parental investment (Parker et al. 1972; Trivers 1972; Kokko and Jennions 2008). Based on this difference in relation to the costs, the sexes may have different selective optima (e.g., see Cox and Calsbeek 2009) and the expression of traits that are selected because they confer benefits to one sex may occur at the expenses of the opposite sex (Arnqvist and Rowe 2005; Hosken and Price 2009; Berg and Maklakov 2012).

It is now clear from studies across several taxa that in some cases selection has pushed male traits that depress female fitness (Fowler and Partridge 1989; Chapman et al. 1995; Crudgington and Siva-Jothy 2000; Crudgington 2001; Blanckenhorn et al. 2002; Wolfner 2002; Kubli 2003; Morrow and Arnqvist 2003; Chapman and Davies 2004; Edvardsson and Tregenza 2005; Eady et al. 2007; den Hollander and Gwynne 2009; Lange et al. 2013; Zuk et al. 2014; Reinhardt et al. 2015). For instance, among the negative effects that mating may imply for females there are influences on female remating rates (Johnstone and Keller 2000; Edvardsson and Tregenza 2005; Edvardsson 2007) and the impact on female longevity (Chapman et al. 1995; Crudgington and Siva-Jothy 2000; Blanckenhorn et al. 2002; Wigby and Chapman 2005; Eady et al. 2007). Interestingly, as a response to harmful male adaptations, females may evolve counter-adaptations to diminish the damage (Rice 1996; Holland and Rice 1999; Arnqvist and Rowe 2002b, a; Rowe and Arnqvist 2002; Edvardsson and Tregenza 2005; Rönn et al. 2007; Cayetano et al. 2011; Gay et al. 2011; Rowe and Arnqvist 2012; Simmons 2014; Dougherty et al. 2017). This evolutionary dynamic process of development of adaptations and counter-adaptations generated by sexually antagonistic selection generates a kind of coevolutionary 'arms race' known as sexually antagonistic coevolution (Holland and Rice 1999; Arnqvist and Rowe 2002a; Chapman et al. 2003; Morrow and Arnqvist 2003; Arnqvist and Rowe 2005; Chapman 2006; Brennan et al. 2007; Rönn et al. 2007; Tatarnic and Cassis 2010; Rowe and Arnqvist 2012; Tanabe and Sota 2014; Brennan and Prum 2015).

The field of sexual conflict has advanced rapidly during the last two decades (Rice and Gavrilets 2014; Zuk et al. 2014). In particular, comparative studies have contributed significantly to understand sexual conflict, sexually antagonistic selection and ensuing sexually antagonistic coevolution (e.g. Arnqvist and Rowe 2002a; Rönn et al. 2007; Perry and Rowe 2012; Brennan and Prum 2015). Experimental evolution approaches have also been instrumental to advance the field: there is now ample evidence that sexually antagonistic arms races are hampered under scenarios where sexual selection is removed or relaxed (Holland and Rice 1999; Martin and Hosken 2003a; Wigby and Chapman 2004; Rice and Holland 2005; Gay et al. 2010; Cayetano et al. 2011; Garcia-Gonzalez 2011). In contrast, our understanding of the role of other selective forces and ecological or

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demographic factors on sexual conflict is very limited (Arbuthnott et al. 2014; Bonduriansky 2014; Carazo et al. 2014; Perry et al. 2017).

In nature, populations are frequently subdivided into demes of various sizes that are interconnected by migration (Levins 1969; Levin 1974; Hanski and Gilpin 1991; Hanski 1999). This spatial structuring of populations has been the focus on intense research over the past decades and there is now overwhelming evidence that metapopulation structure has immense evolutionary and ecological consequences (Hanski 1999; Hanski et al. 2011). However, we know very little about the likely far-reaching implications of population subdivision on the dynamics of sexual conflict. Results from a recent theoretical study shows that metapopulation structure favours the fixation of polyandrous behaviour (Yasui and Garcia-Gonzalez 2016). Rates of female multiple mating could then be higher in subdivided populations than in panmictic populations, which in turn would imply that post-copulatory sexual selection including sperm competition should be more intense in spatially structured populations compared to undivided populations. Following this logic, a prediction would be that sexual conflict should be more intense in metapopulations. However, subpopulations within a metapopulation can act as refuges for different genotypes or strategies that would otherwise be selected against in non-spatially structured large populations, e.g. coexistence of predators and prey, coexistence of different mating system strategists, etc. (Huffaker et al. 1963; Hassell et al. 1991; Tilman 1994; Holyoak and Lawler 1996; Bonsall et al. 2002; Yasui and Garcia-Gonzalez 2016). In other words, metapopulation theory would predict that less competitive genotypes (e.g., in the case of sexual conflict less resistant females or less "manipulative" males) can persist for longer in small subpopulations compared to large undivided populations, which would imply that sexually antagonistic selection is less intense under metapopulation structure. Furthermore, sexual conflict theory predicts more intense sexual conflict in larger populations (Gavrilets 2000; Martin and Hosken 2003b; Gay et al. 2009) and in fact this seems to be the case (Gay et al. 2010). Indeed, the lack of genetic drift and higher levels of genetic variability in large, dense populations, along with higher probabilities for individuals to interact with other individuals (mates and competitors) may fuel sexual antagonistic selection. If so, sexual conflict intensity would be attenuated at the metapopulation level, compared to populations that are not subdivided. This question is one for which empirical testing has been very limited (Martin and Hosken 2003b; Gay et al. 2009; Gay et al. 2010). Even less attention has been given to the influence of population subdivision on the intensity of sexual conflict and sexually antagonistic coevolution; to the best of our knowledge no specific study has so far addressed such question.

In this chapter we address these interesting aspects of sexual conflict evolution. We investigate for the first time the role of spatial structure upon the evolution of sexual conflict traits and their consequences, at the same time that we examine the interactive effects of selection on mating system and metapopulation structure on the evolution of male harm and female resistance. To this end we use an experimental evolution approach carried out on *Callosobruchus maculatus,* a naturally polygamous species that exhibits strong sexual conflict (Crudgington and Siva-Jothy 2000; Crudgington 2001; Rönn et al. 2007; Hotzy and Arnqvist 2009; Gay et al. 2010; Berg and Maklakov 2012). We run an innovative factorial

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experimental design in which both mating system and spatial population structure selection treatments were combined to assess the evolutionary response in a series of male and female life-history and behavioural traits that represent or are connected to male persistence adaptations (manipulative traits or harmful to females' traits) and male resistance counteradaptations.

Material and Methods

Details about the experimental evolution protocol and the biology of the study system are thoroughly described in Chapter 1. Below we describe the methods followed to measure reproductive and life-history traits to assess the evolution of male harm and female resistance in the replicated selection lines evolving under the four distinct selection regimes that we set up in our selection experiment. These selection regimes resulted from the combination of a mating system selection treatment (two levels: monogamy vs. polygamy) and a population spatial structure selection treatment (two levels: presence or absence of population subdivision).

A first set of traits were measured or derived from the first copulation of pairs of virgin individuals However, the first mating may provide limited information on the consequences of divergent interests between the sexes, as females need a minimum of one mating to reproduce. For this reason, a series of complementary analyses have been carried out on traits that were measured or derived from the females' first remating (i.e., second mating). A third set of data was collected to assess female productivity and longevity after lifelong cohabitation with males (continuous exposure to male harassment and mating attempts). Finally, a fourth set of data was taken to assess the baseline longevity of individuals from the different selection lines (i.e., lifespan without influences from conspecifics such as effects mediated by harassment and copulation), to control for any possible differences in intrinsic longevity among the different selection regimes.

1. Baseline longevity

Differences among the different replicated populations in the longevity assays below could be largely determined by intrinsic survival differences, rather than to differences attributable to the ability of individuals to inflict harm or to resist such harm (see below). To take into account this possibility we measured baseline longevity in the selection lines at generation 43. We monitored lifespan in virgin focal males and virgin focal females when they were in isolation, excluding therefore the influence of multiple potential factors affecting longevity (e.g., mate searching and courtsthip costs, influences due to mating injuries in females, influences due to the transfer/receipt of ejaculates, etc.). Individuals from the different selection lines were collected from infested mung beans that were individually isolated in 1.5 ml Eppendorf tubes. These tubes were monitored on a daily basis for adult emergence and subsequent adult longevity. Longevity was measured in a total of 960 individuals distributed in 30 individuals from each sex per line (n= 480 males and 480 females; see Table 5.1).

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2. Traits assayed during (or as a consequence of) the first copulation

Five main response variables were measured (i) copulation latency (time from the moment the male and female were introduced in the vial to the beginning of mating; see below), (ii) copulation duration (iii) female kicking behaviour duration (see below), (iv) female Lifetime Reproductive Success (LRS, lifetime number of offspring produced) and (v) female longevity (number of days that the females were alive after mating).

The assays were carried out at generation 32 of the selection experiment. The mating interactions of 20 focal virgin individuals (10 from each sex) per each of the 16 replicated lines were recorded using a videocamera (HDR-CX405 Handycam, Sony Corporation, Tokio, Japan). Sourcing of virgin individuals was done as specified in Chapter 1, briefly, individually isolating inoculated beans inside 1.5 ml Eppendorf tubes. Each focal individual was paired with a single tester individual of the opposite sex in a small glass container (10mm diameter x 40 mm height). Each couple was allowed 15 minutes to initiate mating. A few pairs of beetles were mating at the end of this period and in these cases, we left the pair undisturbed until the male and female separated. Afterwards, the male was removed and the female was transferred to a small plastic container (30 ml) with approx. 65 beans to allow oviposition. Females remained in these containers until their death, and the containers were kept for later counting of adult offspring production. The videos were analyzed to draw measures of copulation latency, copulation duration and kicking duration. The oviposition containers were checked once daily to note down female longevity. The containers with the newly emerged adult offspring were frozen 29 days after their establishment, allowing enough time for the emergence of the majority if not all offspring produced by females (see Chapter 4). Counting of adult offspring in these containers provided a measure of female LRS. Elytron length (EL), measured following the protocol described in Chapter 2 (section Material and Methods), was used as a proxy of body size for focal and tester males and females. Figure 5.1 provides an outline of this experiment.

The mating behavior of a total of 320 pairs of beetles was videotaped (n = 160 pairs using focal males and 160 pairs using focal females). The protocol followed to generate tester individuals used in this experiment was described in Chapter 1 (section "Tester individuals from near-isogenic lines"). Tester individuals were collected from near-isogenic lines maintained for 35 generations. Focal individuals used in this experiment were sourced from populations subjected to common garden (see Chapter 1, section Common garden breeding) for two generations before the experiment was carried out.

3. Traits assayed on the second copulation (remating) of focal females

We analyzed data on copulation latency, copulation duration and kicking duration gathered from the second copulation of a different set of focal females (n = 77) after 30 generations. The experimental conditions and methodology were identical to those described above for the analysis of the first copulation (i.e., opportunities for remating were given every 24 hours for 9 days). Similarly, sample sizes were identical (a total of 320 pairs screened and videotaped), but only those pairs of beetles that completed a second copulation among the series of opportunities that were given, were included in this analysis. Tester males used in this experiment

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were collected from near-isogenic lines after 33 generations. Focal individuals used in this experiment were sourced from populations subjected to common garden (see Chapter 1, section Common garden breeding) for one generation before the experiment was carried out.

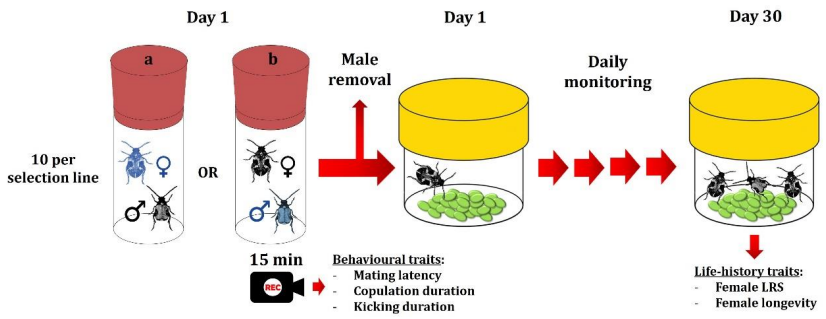

Fig. 5.1. Experimental design to measure behavioural and life-history traits during (or as a consequence of) the first copulation. Each virgin focal individual (in black) was paired with a single tester individual (in blue) of the opposite sex in a small glass container for 15 minutes. Sexual interactions were videotaped and analyzed to extract information about mating latency, copulation duration and kicking duration. After the time allocated for sexual interactions the male was removed and the female was transferred to a small plastic container (30 ml) with beans to allow oviposition. The oviposition container was checked once daily to measure female survival. The container with the newly emerged adult offspring was frozen 29 days after their establishment, and counting of the female LRS was carried out afterwards.

4. Female productivity and longevity under continuous exposure to male harassment and matings.

Male harm and female resistance to male harm was analysed after lifelong sexual cohabitation (i.e. continuous exposure of females to male harassment and mating attempts) after 47 generations. Male harm was estimated in assays in which we measured female productivity and female longevity of standardized tester females housed with focal males (i.e., males from the selection lines), while the evolution of the female's ability to resist the harm was estimated in assays where productivity and longevity were assessed in focal females when they were housed with standardized tester males. Each (1-2 day-old) female (tester or focal) was housed with three males (age ranging from 1 to 4 days old) in a small plastic container (30 ml approx.) with 65 beans approximately for the first 24 hours (day 1). On the second day, the individuals were transferred to a second container with the same amount of fresh beans, where they remained for a week. After that time, the individuals were transferred to a third container with a similar amount of beans, where they remained until female death. This protocol ensured that female had beans *ad libitum* to lay eggs. The containers with the newly emerged offspring were frozen 29 days after the removal of the individuals from each specific vial, to

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ensure that most, if not all, the offspring had emerged from the beans by this time (see Chapter 4). Males that died before the female were replaced with new males to keep constant the ratio of males to females in all containers. We carried out two complementary measurements of productivity. On the one hand, the number of adult offspring produced in the first 24 hours (hereafter, Short-term productivity (STP)) and, on the other hand, the female LRS.

The effect of 10 focal males and the response of 10 focal females per selection line was analyzed (n = 320 (160 per sex)). However, some observations had to be removed from the analysis (see Table 5.1 for details). Figure 5.2 provides an outline of this experiment. Tester individuals used in this experiment were collected from near-isogenic lines after 50 generations. Focal individuals used in this experiment were sourced from populations subjected to common garden (see Chapter 1, section Common garden breeding) for one generation before the experiment was carried out.

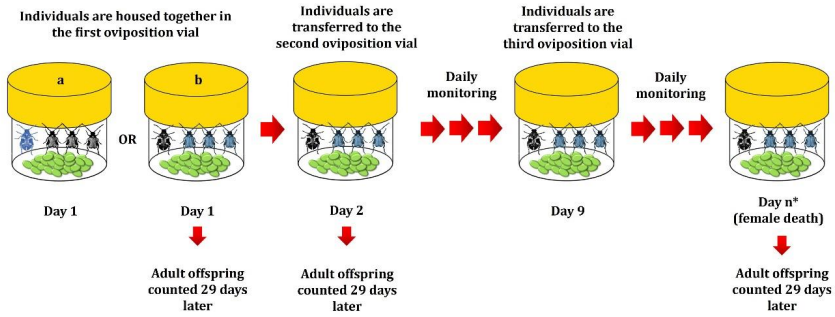

Fig. 5.2. Experimental design to measure the effect of lifelong cohabitation with males on the evolution of male harm and female resistance. Male harm (a) was estimated in assays in which we measured female productivity and female longevity of tester females (in blue) housed with focal males (i.e., males from the selection lines; in black). Female's ability to resist the harm (b) was estimated in assays where females' productivity and longevity were assessed in focal females when they were housed with tester males (in blue). Each female (tester or focal) was housed with three males in a small plastic container (30 ml) with beans for the first 24 hours (day 1). On the second day, the individuals were transferred to a second oviposition container with new beans, where they remained for a week. After that time, the individuals were transferred to a third oviposition container with new beans where they remained until female death. The containers with the newly emerged offspring were frozen 29 days after the removal of the individuals from each specific vial, to ensure that most, if not all, the adult offspring had emerged from the beans by this time (see Chapter 4). The date in which the last container was frozen (day n*) varied depending on when the female died. Males that died before the female were replaced with new males to keep constant the ratio of males to females in all containers.

Statistical analysis

All the analyses were run in R 3.3.2 (R Core Team 2016).

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In the analysis of traits relating to the first mating of females we had data collected from tester females mated to focal males to assess the effects of males on female survival and fitness ('*male harm*'), and data collected from focal females mated to tester males to investigate variation in female resistance to the damage inflicted by males during copulation ('*female resistance'*). The methodology was identical for the analyses of both cases. The response variables mating latency, copulation duration, kicking duration and female longevity were log-transformed while LRS was squared. Linear Mixed Models (LMM) were fitted on the dependent variables using the function '*lmer*' implemented within the package '*lme4*' (Bates et al. 2015). LRS and female longevity were also analyzed using Generalized Linear Mixed Models with Poisson distributions (GLMM), as these variables are counts. When the response of a count variable takes a very high number of values the variable can be treated as continuous variable (Zuur et al. 2009). In our case, both LRS and longevity presented a number of values large enough, especially LRS. For this reason, we run GLMM but also confirmatory LMMs on these variables. In addition, GLMMs were also run for these two variables using the function '*glmmPQL'* from the package '*mass*' (Venables and Ripley 2002) to improve the dispersion of the residuals of the models using a quasipoisson distribution. In all cases both LMMs and GLMMs yielded the same results, and we show here the results pertaining to LMMs.

The models included the following variables as predictors: mating system selection treatment (monogamy/polygamy), population spatial structure selection treatment (metapopulation/no structure), and the interaction of these two factors, as fixed effects, as well as the selection line as a random factor nested within each combination of mating system and population spatial structure (what we call selection regime, see Chapter 1). Male and female body sizes (EL) were included as covariates in all the analyses. Copulation duration was also added as a covariate in the analyses of female LRS and longevity. Finally, female longevity was included as covariate in the analyses of LRS and, and LRS was included in the models were female longevity was the response variable. All the covariates were mean centered to improve the interpretability of regression coefficients, as recommended by Schielzeth (2010).

In the analysis of behavioural traits (latency to copulation, copulation duration and kicking duration) from the second copulation of focal females the three response variables were log-transformed and LMMs were used. The fixed and random factors were the same as those described above. EL was used as proxy of body size and it was also included in the models as a covariate.

In the analyses of female productivity and longevity under continuous exposure to males, the square transformation was applied to the measurements of productivity (STP and LRS), while the data regarding female longevity did not need transformation to meet the assumption of normality of residuals from the models. The fixed and random factors were the same as those previously described. EL was also included as a covariate in all the models. Additionally, female longevity was added as covariate in the models of STP and LRS. In turn, LRS was included as covariate in the models where female longevity was the response variable. Both LMM and GLMMs were run, for the reasons stated above.

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Finally, for the analysis of baseline longevity, LMM models were run on the untransformed data. The above-indicated fixed and random factors were included, and EL was included as a covariate in the models.

We were interested in the contribution of particular effects to variance in the dependent variables (i.e. hypothesis testing) rather than on finding the best model out of many competing ones. Thus, the focus of the analyses was to test the significance of effects. We followed the same protocol in all cases. First, we fitted the full model (the model with all the predictors and their interactions) and tested it against the null model (the model lacking the predictors of interest but including the random structure of the data, i.e., the random factor Selection Line) with a Likelihood Ratio Test (LRT) using the R function '*anova*' with argument test set to '*Chisq*'. It has been suggested that significance tests for individual predictors should only be considered once the full model reveals significance, unless an error-level adjustment for multiple testing is used to avoid inflation of Type-I error (Forstmeier and Schielzeth 2011). We adjusted *p* values for multiple testing using the Benjamini-Hochberg procedure (Benjamini and Hochberg 1995), to correct for such potential source of inflation of Type-I error.

We ran progressively simplified models by removing fixed effects (or their interactions) one-at-a-time using the '*drop1'* function (argument test set to '*Chi*') from the package '*stats*' (R Core Team 2016), and testing the effect of removal of each term on the change in model deviance using likelihood ratio tests and maximum likelihood (Bolker et al. 2009). The final model included the significant effects (alpha criterion of 0.05), and we also always retained in the final model the fixed factors mating system and population spatial structure plus the random factor Selection Line, regardless of the contribution of these factors, to account for the structure of the experimental design and the hierarchical structure of the data (i.e., for the fact that the data is grouped by the random factor within each combination of mating system and population structure selection levels). The LRT for the non-significant effects was calculated using the '*drop1'* function after adding the particular non-significant effect to the final model.

While significance of the fixed effects was calculated using maximum likelihood as described above, parameter estimates (coefficients, estimates) of the fixed and random effects in the final model were calculated using Restricted Maximum Likelihood (REML), as it has been suggested (Zuur et al. 2009). The random effect was tested with a likelihood ratio test (Lynch and Walsh 1998; Bolker et al. 2009), comparing the final model with the random term and using REML to the model without the random factor. The degrees of freedom of all the LRT and F-tests was always 1 because *drop1* compares two models (with and without the tested effect). Sample sizes have been indicated above in sections regarding the assayed and they have also been included in the tables regarding the analysis of each response variable.

Pairwise comparisons among the levels within the explanatory fixed factors included in the models were carried out by mean of post-hoc Tukey tests using the function 'lsmeans' implemented in the package with the same name (Lenth 2016).

The marginal and conditional R^2 values for the final LMM model were calculated with the function '*sem.model.fits*' implemented in the package '*piecewiseSEM*'

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(Lefcheck 2016). We checked that the assumptions of the analysis (normality and homogeneity of residuals) were fulfilled by visually inspecting qqplots and plots of the distribution of the residuals against fitted values.

Sample sizes in the analyses differed from those stated above as follows. The general protocol for the detection and removal of influential observations and outliers (see Chapter 2) was applied before running the models. Moreover, for the assays from the first copulation pairs that did not mate in the time allowed were not included (n = 8; 4 for the focal males and 4 for the focal females sets, respectively). A few additional individuals were removed because of missing information (e.g. lack of individual body size measurement due to sample deterioration in 4 individuals; 2 for the focal males and 2 for the focal females sets, respectively). Following a conservative criterium, females that did not produce any offspring were also excluded (n = 5; 3 from the dataset of focal males and 2 for focal females respectively) because such a low rate of infertile matings can be due to permanent or temporal male or female infertility problems (Garcia-Gonzalez 2004 and see Chapter 3). In the analyses of female productivity and longevity after lifelong exposure to males a total of 28 observations were removed a priori from the analyses due to experimental mishaps with the individuals or the collection of information regarding some variables. We also excluded from the analyses of LRS in these assays observations in which LRS values were equal to zero (n = 3; 2 in the dataset of tester females and 1 in the dataset of focal females). Likewise, a few observations (4; 3 in the dataset of tester females and 1 in the dataset of focal females) were excluded in the analyses of female longevity from these assays because of no offspring production. Finally, in the analyses of baseline longevity 16 observations were excluded because we could not measure some of the experimental variables included in the models due to sample deterioration or mishaps (e.g., lack of data for precise date of death). Table 5.1 provides full details about initial and final sample sizes and the reasons for the reductions of sample size when applicable.

We also run the analyses including the data highlighted as influential outliers to assess whether the inclusion or exclusion of those data rendered different results. Results were qualitatively identical before and after the removal of influential outliers within each of the analyses included in this chapter. We just show here the results of the main analysis excluding influential outliers, because the models from these data meet better the assumptions of normality and homoscedasticity.

We report mean ± standard error values throughout. Tables are reported after the references. Parameter estimates and other details of the models run can be found in the Appendix at the end of the chapter.

Results

1. Baseline longevity

Neither the mating system, nor the spatial structure or their interaction had a significant effect on the baseline longevity of either sex (see table 5.2). Unsurprisingly, baseline longevity was significantly affected by body size in both sexes (males: LRT = 35.45, df = 1, $p < 0.0001$, females: LRT = 24.61, df = 1, p <

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0.0001) with larger individuals living for longer regardless of the selection regime under which they had evolved (Fig. 5.3). Table 5.3 shows the means for male and female baseline longevity.

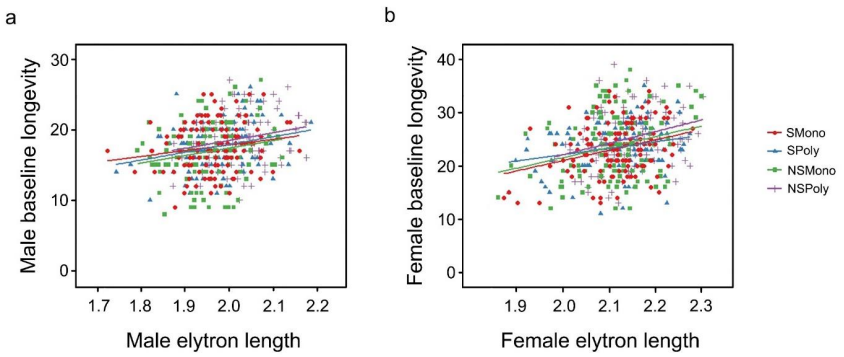

Fig. 5.3. Relationship between body size (in millimeters) and baseline longevity (in days) for males (a) and females (b). The color of the points represents each of the four selection regimes resulting from the combination of mating system and population spatial structure selection treatments.

2. Traits assayed during (or as a consequence of) the first copulation

2.1. Evolution of sexually selected and sexual conflict traits in males, including male harm (effects of focal males on tester females' fitness).

Latency to copulation

A significant interaction between mating system and population spatial structure was found (LRT = 4.88, df = 1, p = 0.03, Fig. 5.4a). In absence of spatial structure, the mating latency of polygamous males was shorter than that from monogamous males, while this pattern was reversed in metapopulations. However, this interaction was not significant after the correction for multiple testing, and besides, post-hoc Tukey tests informed that none of the differences between groups was significant (see table 5.4). None of the main effects, or the body size of the individuals of either sex influenced copulation latency (see table 5.5). Table 5.6 shows the means for mating latency for each of the groups analyzed.

Copulation duration

Copulation duration was significantly affected by both mating system (LRT = 6.98, df = 1, p = 0.008) and population spatial structure selection treatments (LRT = 6.17, df = 1, p = 0.01, Fig. 5.4b). Copulations by males from polygamous selection lines were longer than copulations from males from monogamous selection lines (when both types of males mated to standardized females). Additionally, the duration of the copulation was higher in populations without population spatial structure. The interaction between the two selection treatments was not

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significant (see table 5.5). Male body size had a significant effect on mating duration (LRT = 7.68, df = 1, p = 0.0056, Fig. 5.4c). The larger the male, the longer the duration of the copulation. The effect of female body size was marginally non-significant (LRT = 3.83, df = 1, p = 0.0502, Fig. 5.4d), and in this case the larger the female the shorter the copulation duration. Table 5.6 shows the means for copulation duration for each of the groups analyzed.

Kicking duration

Neither the mating system, nor the population spatial structure or their interaction had a significant effect on the duration of the kicking behavior (see table 5.5). However, this reproductive trait was significantly affected by the body size of males (LRT = 15.37, df = 1, p < 0.0001, Fig. 5.4e) and females (LRT = 15.22, df = 1, p < 0.0001, Fig. 5.4f). Male body size was positively correlated with the duration of the kicking behavior while on the contrary female body size was negatively correlated with its duration. Table 5.6 shows the means for kicking duration for each of the groups analyzed.

Female lifetime reproductive success

None of the selection treatments or their interaction significantly affected female LRS. Similarly, the effects of female body size, copulation duration or female longevity on the LRS were non-significant (see table 5.5). Interestingly, male body size had a significant effect on female LRS (LRT = 6.72, df = 1, p = 0.01). The larger the male, the more adult offspring produced her mate, regardless of selection history (Fig. 5.4g). However, significance was lost after applying the correction for multiple testing. Table 5.6 shows the means for female LRS for each of the groups analyzed.

Female longevity

Female body size was the only variable significantly predicting female longevity (LRT = 13.31, df = 1, p = 0.0003). Females with larger body sizes lived for longer (Fig. 5.4h and table 5.5). Table 5.6 shows the means for female longevity for each of the groups analyzed.

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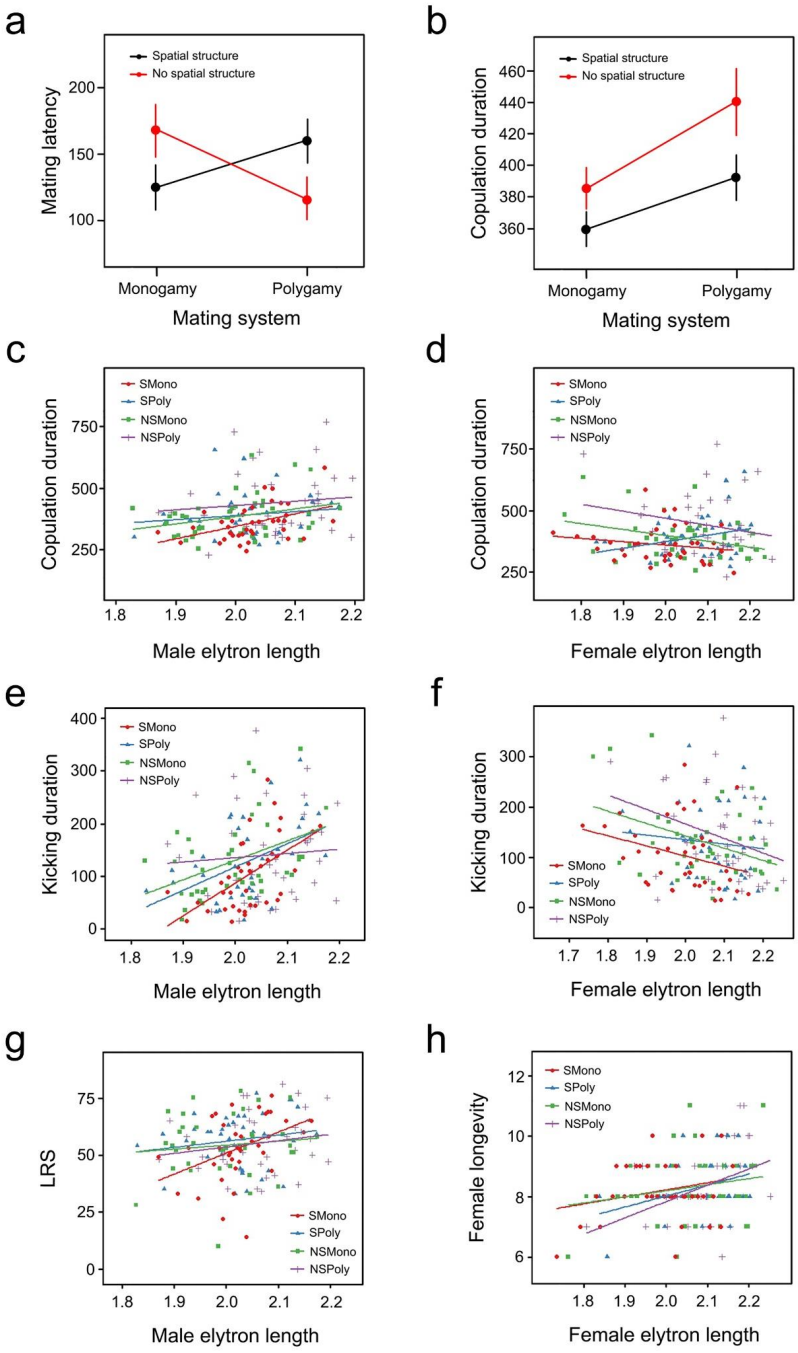

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Fig. 5.4. Panel of figures related to male harm (effects of focal males on tester female behavioural and life-history traits) during the first copulation. Main and interactive effects of mating system (monogamy vs. polygamy) and population spatial structure (metapopulation structure vs. no structure) selection treatments on mating latency (in seconds) (a) and copulation duration (in seconds) (b). The images depict the mean (±1SE) of each response variable in each selection regime (the result of the combination of the two selection treatments: SPoly, NSPoly, SMono, NSMono), calculated across the different lines (units of replication) for that particular selection regime. Data from populations with spatial structure are shown in black while data from populations without spatial structure are shown in red. Panels c-h show the relationship between the individuals body size and the different response variables as follows: relationship between copulation duration and male and female body sizes (panels c and d, respectively); relationship between kicking duration and male and female body sizes (panels e and f, respectively); relationship between male body size and female LRS (g); relationship between female body size and female longevity (h). The color of the points represents each of the four selection regimes resulting from the combination of mating system and population spatial structure selection treatments.

2.2. Evolution of female traits, including female resistance traits to male harm (effects of tester males on focal females' fitness).

Latency to copulation

Neither the mating system, nor the population structure or their interaction, or the body size of the individuals had a significant effect on mating latency (see table 5.7). Table 5.8 shows the means for mating latency for each of the groups analyzed.

Copulation duration

Copulation duration was significantly affected by male body size (LRT = 5.85, df = 1, p = 0.02). Here, the larger the male, the shorter the duration of the copulation (Fig. 5.5a), that is, the reverse of the pattern found when tester females were mated to focal males. However, this effect is no longer significant after applying the correction for multiple testing. None of the other terms in the model showed a significant effect on copulation duration (see table 5.7). Table 5.8 shows the means for copulation duration for each of the groups analyzed.

Kicking duration

Population spatial structure selection history had a significant effect on kicking duration (LRT = 4.41, df = 1, p = 0.04), such that females from structured populations kicked for longer than females from non-structured populations (Fig 5.5b). Nevertheless, the effect of population structure was no longer significant after applying the correction for multiple testing. Neither the mating system, nor its interaction with population spatial structure had a significant effect on kicking duration (see table 5.7), but the time that females were trying to dislodge the males was significantly affected by male body size (LRT= 7.96, df = 1, p =0.005, Fig. 5.5c): the larger the male, the longer the kicking duration. Female body size on the other hand did not seem to influence kicking duration (see table 5.7). Table 5.8 shows the means of kicking duration for each of the groups analyzed.

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Female lifetime reproductive success

The number of adult offspring produced by focal females during their entire lifespan was significantly affected by population spatial structure (LRT = 4.40, df = 1, p = 0.04) with females from structured populations producing overall greater numbers of offspring than females from non-structured populations (Fig 5.5d). However, such effect of population spatial structure was no longer significant once the correction for multiple estimations of the significance was applied.

Female longevity was significantly related to female LRS (LRT = 10.36, df =1, p =0.0013), such that females that lived for longer produced fewer offspring, indicating, as we know from other assays in this thesis (and see below the analysis of female longevity), that reproduction entails a longevity cost (i.e., higher fecundity and offspring production is associated to lower longevity) (Fig. 5.5e). The remaining terms in the models did not have a significant effect on the female LRS (see table 5.7). Table 5.8 shows the means for female longevity for each of the groups analyzed.

Female longevity

None of the selection treatments or their interaction affected significantly female longevity (see table 5.7). Male body size did not affect female longevity either, while the size of the females did show a statistically significant effect (LRT = 18.29, df = 1, p < 0.0001), with larger females living for longer (Fig 5.5f). Copulation duration did not to have a significant effect on the longevity of the focal females (see table 5.7). As expected, however, a female's LRS significantly affected her longevity (LRT = 17.44, df = 1, p < 0.0001, Fig. 5.5e), with females that produced more offspring living less time. Table 5.8 shows the means for female longevity for each of the groups analyzed.

Fig. 5.5. Panel of figures related to female resistance (effects of tester males on focal female behavioural and life-history traits) during the first copulation: panels a, c, e and f show the relationship between the different response variables and certain covariates as follows: (a) relationship between copulation duration and male body size; (c) relationship between kicking duration and male body size; (e) relationship between female LRS and female longevity; (f) relationship between female body size and female longevity. The color of the points represents each of the four selection regimes resulting from the combination of mating system and population spatial structure selection treatments. Additionally, panels b and d show the main and interactive effects of mating system (monogamy vs. polygamy) and population spatial structure (metapopulation structure vs. no structure) selection treatments on kicking duration (in seconds) (b) and female LRS (d). The images depict the mean (±1SE) of each response variable in each selection regime (the result of the combination of the two selection treatments: SPoly, NSPoly, SMono, NSMono), calculated across the different lines (units of replication) for that particular selection regime. Data from populations with spatial structure are shown in black while data from populations without spatial structure are shown in red.

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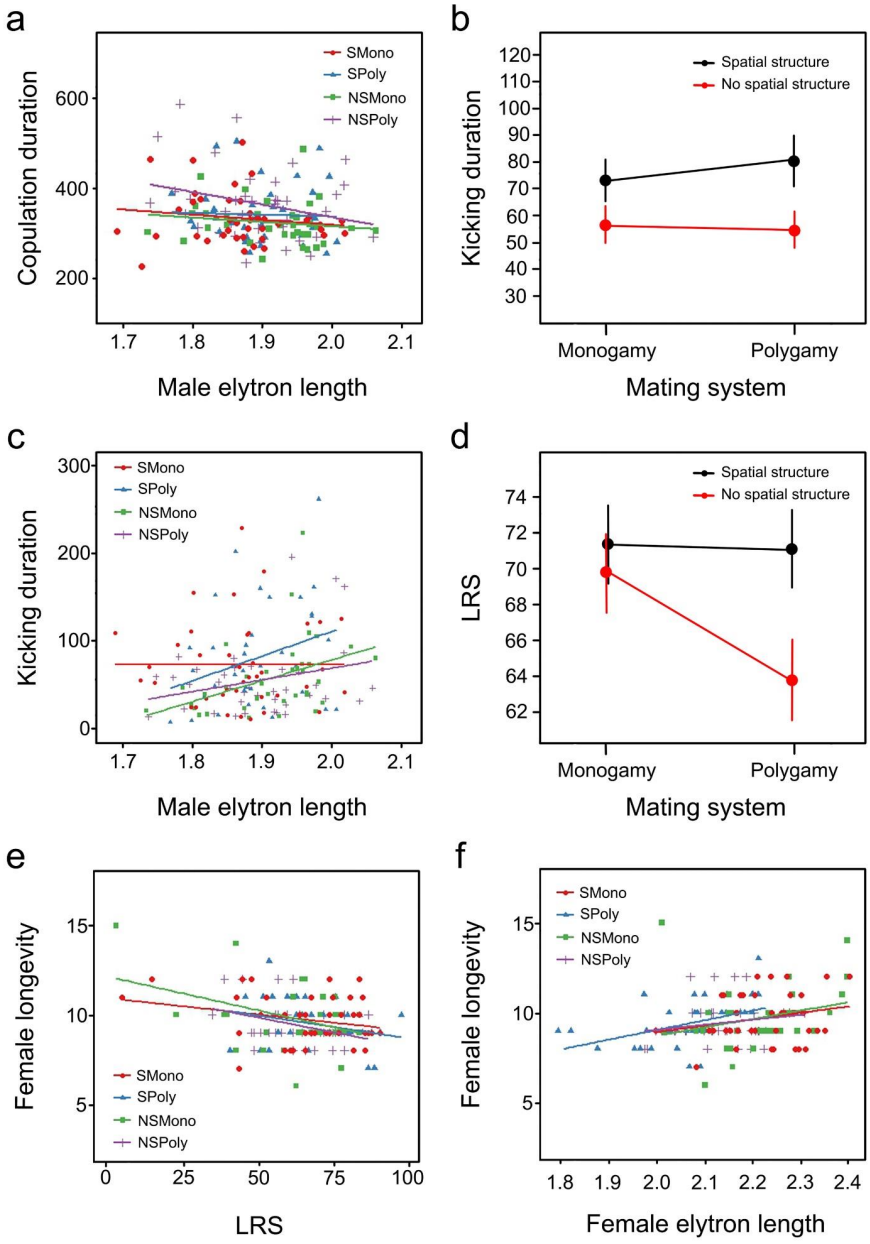

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3. Female traits assayed during the second copulation of focal females

Latency to copulation

None of the main selection treatments or their interaction had a significant effect on mating latency (see table 5.9). The effect of the female body size was marginally non-significant (LRT = 3.81, df = 1, p = 0.0509); the pattern was that the larger the (non-virgin) female the longer the male needed to succeed in their attempts to copulate with her (Fig. 5.6a). Table 5.10 shows the means for mating latency for each of the groups analyzed.

Copulation duration

Neither the selection treatments, nor the selection regimes resulting from their interaction, or female body size had a significant effect on the duration of the second copulation (see table 5.9). Table 5.10 shows the means for copulation duration for each of the groups analyzed.

Kicking duration

The effect of the interaction between the two selection regimes was marginally non significant (LRT = 3.71, df = 1, p = 0.0542). Mating system selection history did not affect the kicking duration (see table 5.9). However, similarly to what happens in the first copulation of females, population spatial structure selection history has a significant effect on the time that the females where trying to dislodge the males (LRT = 8.25, df = 1, p = 0.0041); females from structured populations kicked for longer than females from populations without spatial structure (Fig. 5.6b). Female body size did not affect kicking duration (see table 5.9). Table 5.10 shows the means for kicking duration for each of the groups analyzed.

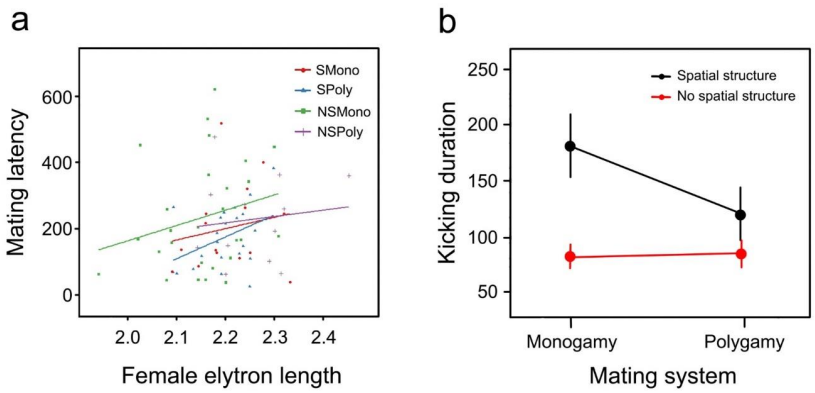

Fig. 5.6. Female resistance assessed from the effects of tester males on focal female behavioural traits during their second copulation. (a) Relationship between female elytron length (in milimetres) and mating latency (in seconds) for each of the four selection regimes established (resulting from the combination of mating system and population spatial structure selection treatments). (b) The main and interactive effects of mating

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system (monogamy vs. polygamy) and population spatial structure (metapopulation structure vs. no structure) selection treatments on kicking duration (in seconds). The image depicts the mean (±1SE) of the time taken for females to dislodge the male at the end of copulation in each selection regime (the result of the combination of the two selection treatments: SPoly, NSPoly, SMono, NSMono), calculated across the different lines for that particular selection regime. Data from populations with spatial structure are shown in black while data from populations without spatial structure are shown in red.

4. Female short-term productivity, LRS and longevity under continuous exposure to males.

4.1. Evolution of sexually selected and sexual conflict traits in males, including male harm (effects of focal males on the fitness of tester females).

Short-term productivity and LRS

There was an interaction between mating system and population spatial structure explaining STP (LRT = 4.93, df = 1, p = 0.03, Fig. 5.7a) (Table 5.11). STP was higher in non-structured populations compared to structured populations but only under the absence of sexual selection (monogamy selection history) (see Fig. 5.7a, Table 5.11 and Table 5.12). This interaction, however, was not significant after correcting for multiple p estimates (see Table 5.11). For the analysis of LRS, neither the mating system nor the population spatial structure or their interaction had a significant effect on female LRS, though the effect of mating system was marginally non significant (see table 5.11) with females exposed to males which have evolved under polygamy having slightly higher values of LRS (Fig. 5.7c). Female body size influenced significantly STP (LRT = 14.61, df = 1, p < 0.0001) and LRS (LRT = 4.91, df = 1, p = 0.03), with larger females producing more offspring not only in the first 24 hours after copulation (Fig. 5.7b), but also along their whole lives (Fig. 5.7d). However, in the case of female LRS the effect was no longer significant after correcting for multiple probability estimates. Female longevity did not affect significantly STP (see table 5.11), but had a highly significant effect on LRS with long-lived females producing greater numbers of offspring (LRT = 24.00, df = 1, p < 0.0001, Fig. 5.7e). Table 5.13 shows the means for short-term productivity and female LRS for each of the groups analyzed.

Female longevity

Regarding female longevity, we found a significant interaction between mating system and population spatial structure selection treatments (LRT = 5.79, df = 1, p = 0.016, Fig. 5.7f). Females mated to males that evolved under monogamy in metapopulations lived longer than females mated to monogamous males from non-structured populations. While the difference between structured and non-structured populations was significant under monogamy, the polygamous populations (structured or not) did not differ significantly (see Table 5.14). Moreover, males from monogamous and polygamous selection lines differed in their effects on female longevity but only when they had been evolving in conditions of population spatial structure (see Table 5.14). Female body size was positively and significantly related to female longevity (LRT = 7.03, df = 1, p = 0.008, Fig.5.7g). LRS also showed a significant and positive correlation with female

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longevity (LRT = 26.66, df = 1, $p < 0.0001$, Fig. 5.7e). Table 5.13 shows the means for female longevity for each of the groups analyzed.

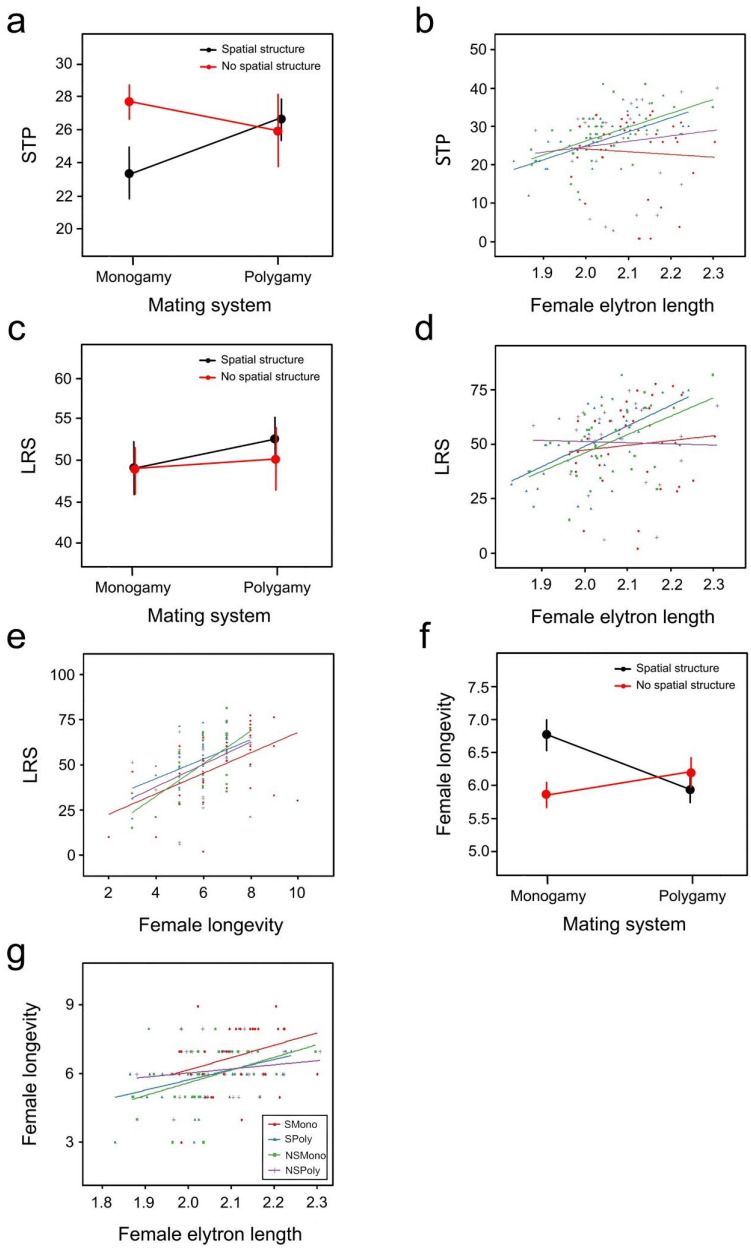

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Fig. 5.7. Panel of figures related to the effects of focal males on tester females' fitness (productivity and longevity) after continuous exposure to males. Panels a, c and f show the main and interactive effects of mating system (monogamy vs. polygamy) and population spatial structure (metapopulation structure vs. no structure) selection treatments on short-term productivity (a), female LRS (c) and female longevity (f). These three panels depict the mean (±1SE) of each response variable in each selection regime (the result of the combination of the two selection treatments: SPoly, NSPoly, SMono, NSMono), calculated across the different selection lines for that particular selection regime. Data from populations with spatial structure are shown in black while data from populations without spatial structure are shown in red. Panels b, d, e and g show the relationship between the different response variables and covariates as follows: (b) relationship between short-term productivity and female body size; (d) relationship between female LRS and female body size; (e) relationship between female LRS and female longevity; (g) relationship between female body size and female longevity. The color of the points represents each of the four selection regimes resulting from the combination of mating system and population spatial structure selection treatments.

4.2. Evolution of female traits, including female resistance traits to male harm (effects of tester males on the fitness of focal females).

Short term productivity and LRS

None of the two selection treatments or their interaction had a significant effect on STP or LRS (see table 5.15). The female's body size significantly affected the number of adult offspring produced by her in the first 24 hours after mating (LRT = 17.12, df = 1, $p < 0.0001$, Fig. 5.8a) as well as the number of adult offspring produced along her lifespan, that is, LRS (LRT = 30.92, df = 1, $p < 0.0001$, Fig. 5.8b). Female longevity was not related to STP (see table 5.15), but it significantly explained female LRS (LRT = 18.69, df = 1, $p < 0.0001$), as it happened to the tester females exposed to focal males. Long-lived females had higher values of LRS (Fig. 5.5.8d). Table 5.16 shows the means for STP, LRS and longevity for each of the groups analyzed.

Female longevity

Neither the mating system selection treatment nor its interaction with the population spatial structure selection treatment significantly explained female lifespan (table 5.15). Female longevity was affected by population spatial structure selection history (LRT = 5.74, df = 1, $p = 0.02$), with females from structured populations exhibiting higher LRS than females from non-structured populations (Fig. 5.8c), but this effect was no longer significant after correcting for Type I error (see table 5.15). Female body size did not have a significant effect in this case. Finally, again LRS and female longevity were positively associated (LRT = 16.09, df = 1, $p < 0.0001$, Fig. 5.8d). Table 5.16 shows the means for female longevity for each of the groups analyzed.

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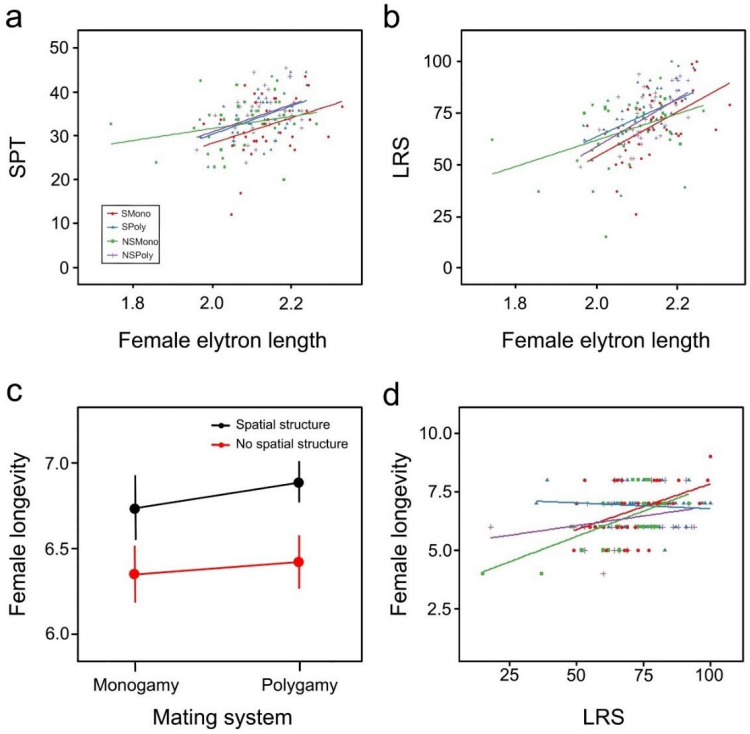

Fig. 5.8. Panel of figures related to the effects of tester males on focal females' fitness (short-term productivity, LRS and longevity) after continuous exposure to males. Panels a, b and d show the relationship between the response variables and covariates as follows: (a) relationship between short-term productivity and female body size (in milimetres); (b) relationship between female LRS and female body size; (d) relationship between female longevity (in days) and female LRS. The color of the points represents each of the four selection regimes resulting from the combination of mating system and population spatial structure selection treatments. Additionally, panel (c) shows the main and interactive effects of mating system (monogamy vs. polygamy) and population spatial structure (metapopulation structure vs. no structure) selection treatments on female longevity. The image depicts the mean (±1SE) of the number of days that females were alive after mating and ovipositing under the experimental conditions (see text) for each of the selection regimes from where the females were sourced (the result of the combination of the two selection treatments: SPoly, NSPoly, SMono, NSMono), calculated across the different lines for that particular selection regime. Data from populations with spatial structure are shown in black while data from populations without spatial structure are shown in red.

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Discussion

The evolutionary interests of males and females over mating and reproduction often differ (Parker et al. 1972; Trivers 1972; Parker 1979; Parker 2006). Consequently, males and females generally follow different reproductive strategies to maximize their fitness, in some cases, even at expenses of the other sex (Clutton-Brock and Parker 1995; Stockley 1997; Hosken et al. 2001; Morrow et al. 2003; Hotzy and Arnqvist 2009; Berg and Maklakov 2012). Such sexual conflict frequently leads to the evolution of adaptations in one sex and counter-adaptations in the other sex, which may in turn lead to a coevolutionary 'arms race' known as sexually antagonistic coevolution (Holland and Rice 1999; Crudgington and Siva-Jothy 2000; Crudgington 2001; Hosken et al. 2001; Arnqvist and Rowe 2002b, a; Rowe and Arnqvist 2002; Rönn et al. 2007; Perry and Rowe 2012, 2014; Wilson and Tomkins 2014).

Identifying the proximate causes driving sexual conflict dynamics has been the focus of recent research (Chapman et al. 2003; Martin and Hosken 2003b; Arnqvist and Rowe 2005; Gay et al. 2009; Gay et al. 2010; Cayetano et al. 2011; Gay et al. 2011; Perry et al. 2017). However, theoretical and empirical research to assess the potential role of presumably important ecological and demographic factors, such as population spatial structure, on sexual conflict dynamics, is lacking. Thus, although our understanding of the coevolution of male harm and female resistance has increased in the last decades (e.g. Holland and Rice 1999; Rönn et al. 2007; Cayetano et al. 2011; Gay et al. 2011), there are important gaps in knowledge in the field. The links between mating system evolution and population spatial structure have been recently investigated from a theoretical point of view by Yasui and Garcia-Gonzalez (2016). However, to date a study exploring theoretically or empirically the effects of both factors on sexual conflict dynamics is lacking, to the best of our knowledge. Here, we implement an experimental evolution approach using the seed beetle *Callosobruchus maculatus* to fill this gap. We investigate the independent effects of variation in mating system selection (polygamy versus monogamy), and consequent influence of the presence/absence of sexual selection, and variation in population spatial structure (metapopulation structure versus no metapopulation structure), as well as their interactive effects, on the evolution of sexual conflict dynamics related to male-induced harm to females and female resistance to male harm.

Behavioural traits

Latency to copulation

Mating latency may reflect on the one hand, male's attractiveness or their ability to manipulate females for mating, but also, on the other hand, it may be understood as a reflection of female resistance to male manipulation. We did not find any evidence of a differential response in relation to mating latency for either sex regardless of the selection regime under which the individuals evolved. Therefore, our results in relation to this trait suggest that male's attractiveness and female resistance to male manipulation have not diverge among our selection regimes. This lack of difference regarding the manipulative ability of males which have evolved under a monogamous or polygamous mating system is in concordance with the results yielded by the study carried out by Gay et al. (2010) to evaluate

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the evolution of male harm and female resistance in the same species after the reintroduction of sexual conflict in populations which have been forced to evolve under monogamy. These authors suggested that males from either of their selection regimes were equally good in their ability to manipulate females for mating.

It is important to stress here that the results from analyses related to the first copulation of pairs of virgin individuals the lack of expected differences in mating latency may be explained when we take into account that females must copulate at least once to produce offspring. Therefore, there is no reason to think that females from polygamous selection regimes should exhibit increased resistance to this (first) mating. Nevertheless, we also carried out the analysis of latency to copulation during the second mating of another subset of focal females which have evolved under the same selection regimes, and we also failed to detect increased mating latencies for females from polygamous regimes in that case.

The fact that the second copulation is likely more informative to infer divergent interests between the sexes is illustrated by the result that larger focal females were able to resist matings more (longer mating latencies) than smaller females. Such relationship between female body size and mating latency was not found in the first copulation, probably because all females are eager to mate a first time to reproduce.

Despite the role of the pericopulatory kicking behavior remains controversial nowadays (see below), it has been suggested that female kicking behaviour may help females to prevent males to get engaged in copulations, rather than being a behaviour to shorten mating, as traditionally assumed (Wilson and Tomkins 2014). If so, perhaps a large female body size allows the females to be more efficient keeping unwanted mates at bay. Regardless, of the implications of kicking behaviour, our results indicate that this is the case.

Copulation duration

In the females' first copulation males from polygamous selection lines engaged standardized tester females in longer copulations than males from monogamous selection lines. This result suggests that males under polygamy selection are selected to gain higher control over copulation (Parker 1979; Holland and Rice 1999; Hotzy and Arnqvist 2009). In addition, a very interesting result in our experiments pertaining to the first copulation is that copulation duration was longer in populations without spatial structure, though it is unclear why copulations would be expected to be longer in both monogamous and polyandrous structured populations. In *C. maculatus*, longer copulations are related to the transfer of larger volumes of ejaculate (Edvardsson and Canal 2006). Several compounds from the ejaculate, produced in different parts of the male reproductive tract, have seen to affect the female receptivity and their oviposition rate in this and other closely related species, influencing male competitive reproductive success (Savalli and Fox 1999; Yamane et al. 2008; Yamane and Miyatake 2010a, c, b; Yamane 2013; Yamane et al. 2015). Savalli and Fox (1999) also determined that the sperm supply is one of the factors which determine the female propensity to remate. Male *C. maculatus* presents last male sperm precedence, thus preventing females from remating is a key factor to increase male

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fitness (Eady 1991; Eady 1994; Eady 1995). With all this in mind, by being able to increase copulation duration, males from non-structured populations could decrease female remating rates and influence to a large extent female reproduction. Despite we detected an effect of the selection treatments on the duration of the first copulation of tester females exposed to focal males, such an effect was absent when the first and the second copulations of focal females exposed to standardized tester males were analyzed. Future investigations will focus on the reasons underlying such differences.

In some species copulation duration is known to be determined by body size. In *Drosophila melanogaster* for example, copulation duration seems to be highly contingent on female body size and much less dependent of male body size (Lefranc and Bundgaard 2000). In our analysis of the effect of focal males on female reproductive behaviour during the first copulation, the body size of males and females showed a clear and opposite effect on the duration of copulation. While a large male body size led to longer copulations, a large female body size tended to shorten copulation. These effects may be a clear reflection of the competition between sexes for the control of copulation. While males would attempt to increase copulation duration to increase their fitness, females' interest may lie in shortening copulation duration once they have received enough sperm to fertilize the eggs and to avoid unnecessary injuries inflicted by the male aedeagal spines during mating (Crudgington and Siva-Jothy 2000; but see Edvardsson and Canal 2006). However, when we analyze the response of focal females to tester males, we did not detect such effects for male and female body sizes. Female body size did not have any effect on the duration of copulation, and contrary to what we found in the analysis of the effect of focal males, actually large male body size was associated to shorter copulation durations. The reasons underlying these contrasting results warrant further investigation.

Kicking duration

Towards the end of the copulation, female *Callosobruchus maculatus* starts to kick the male using the hind legs (Crudgington and Siva-Jothy 2000; Crudgington 2001). The function of this conspicuous female behavior remains unclear still nowadays. Initially, the results of several studies suggested that females kick the mounted males to dislodge them once the mating duration is approaching the female optimum, shortening mating duration and likely minimizing the damage caused during copulation by male genitalia, which is known to have a negative impact on female lifespan (Crudgington and Siva-Jothy 2000; Edvardsson and Tregenza 2005; Gay et al. 2010; van Lieshout et al. 2014).

Nevertheless, the results of the study carried out by Wilson and Tomkins (2014) showed that female kicking not only does not shorten copulation but also it boosts the damage that the male spiny genitalia inflict to the female reproductive tract before the onset of kicking, decreasing in turn their longevity. Wilson and Tomkins (2014) pointed out that males, and not females, control the kicking duration and they suggested that female kicking may be useful to prevent males from starting new copulations, but it is a futile attempt to shorten the duration of the mating event once it has started. More recently, this idea has been supported by an elegant experiment carried out by Dougherty and Simmons (2017), in which X-ray micro-CT scanning was used to analyze flash-frozen pairs at different times during

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mating. Dougherty and Simmons' study (2017) revealed that there is some degree of temporal separation between the onset of wounding and the onset of kicking, supporting in that sense recent suggestions that kicking is not an effective female counter-adaptation to reduce copulatory wounding in this species.

In order to understand the elusive function of kicking behaviour in *C. maculatus* it seems paramount to understand the function of male aedeagal spines. However, the function of the species' spiny male genitalia also remains controversial. It is believed that the spines may function as anchor during copulation to hinder take-overs from rival males and to prevent females from terminating copulation before the duration that is optimal to the male (Edvardsson and Tregenza 2005; Edvardsson and Canal 2006), though a comparative study has shown that species with longer aedeagal spines did not stay in copulation for longer (Ronn and Hotzy 2012).

In our study, when focal males were mated to tester females, the individuals' body size affected the extent of female kicking behaviour. These results indicate once more that the size of the individuals plays a decisive role determining the control of copulation duration. An important conclusion of our results is therefore that body size is a key sexual conflict trait in *C. maculatus*. Nevertheless, there are nuances in regards to the role of body size on kicking behaviour. The same positive effect of male body size on kicking duration was found in the analysis of the response of focal females. However, in this case female body size seemed not to determine kicking behaviour.

Additionally, focal females from structured populations kicked for longer than females from non-structured populations, and this pattern was consistent across the first and second copulation of females. It is worth to be noted that both tests were independent because they were run at different times and using different sets of females, which provides increased confidence in the results. Recent studies have suggested that the relatedness and/or familiarity among individuals modulates sexual conflict, such that higher relatedness and/or familiarity result in a decrease of male harm to females (Carazo et al. 2014; Hollis et al. 2015; Pizzari et al. 2015; Le Page et al. 2017; Łukasiewicz et al. 2017; Lymbery and Simmons 2017). This, applied to our selection conditions, where it could be assumed that population structure leads to higher relatedness among individuals (though this is debatable due to the 20% migration rates imposed among subpopulations), would predict more kicking in panmictic populations than subdivided populations, at least in polygamous populations (where sexual conflict is present). We however, have observed the reversed pattern in our data. It is also not clear why structured and non-structured monogamous populations (where sexual conflict is absent) differ in kicking behaviour. More research is needed to understand the drivers of these differences, but what is clear is that our results from two independent tests reveal some interesting and potentially far reaching effects of population spatial structure on behaviours that are key to determine individual fitness.

Life-history traits

Female productivity: short-term productivity and lifetime reproductive success

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Female productivity is one of the most informative traits to evaluate the sexes tug of war because it ultimately determines female fitness. Several studies have found that under monogamy females exhibit a higher reproductive rate or fecundity than females evolving under polygamy, mainly because under monogamy females are released from paying the costs associated to mating with harmful males (Holland and Rice 1999; Martin et al. 2004). On the other hand other studies, such as Martin and Hosken's (2003a) on the dung fly *Sepsis cynipsea*, have found no significant differences in terms of female LRS between monogamous and polygamous mating selection lines. Thus, the evidence is mixed (and see Chapter 4 for a more detailed discussion on these aspects).

The analysis of the effect of focal males on female LRS (analysis of the evolution of male harm) did not detect any effect of the mating system, population spatial structure or their interaction on this trait after a single copulation. Thus, overall there was no clear support for expectations stemming from sexual conflict regarding the evolution of male harm (e.g., lower LRS for tester females exposed to polygamous males, compared to tester females exposed to monogamous males).

The analysis of the response of focal females to tester males (analysis of the evolution of female resistance) showed a signal for an effect of population spatial structure on female LRS after a single copulation. Females from structured populations presented higher values of LRS than females from non-structured populations, but the effect was not significant after correcting for multiple estimates of probability. The effect was also absent when the response of focal females was assessed when they were continuously exposed to males.

Thus, our results suggest that the selective pressures arising from sexual selection, through mating system, and population structure did not have noticeable effects on the productivity of females from our selection regimes.

Individuals' body size did not affect significantly female productivity after a single copulation. In fact, we only detected a subtle effect of male body size on female LRS when tester females were engaged in copulation with focal males. The results seemed to suggest that female LRS increased with male body size. In *C. maculatus*, larger males are known to transfer larger ejaculates, and it is also known that some compounds in the ejaculates induce female oviposition (e.g. Yamane and Miyatake 2010a, c; Yamane 2013), which perhaps may be translated into higher LRS under favourable conditions. Nevertheless, two aspects must be taken into account. On the one hand, we did not measure female fecundity, so we do not know if the oviposition rate was higher for females mated to larger males, and on the other hand, the effect of male body size on female LRS was no longer significant after applying the Benjamini-Hochberg correction for multiple estimates, thus we should be cautious with the interpretation of this subtle effect. When females were continuously exposed to male harassment however, female body size showed a positive effect in relation to their productivity. Such a significant effect was constant when the response (in the first 24 hours or along the entire female lifespan) of focal females continuously exposed to focal males was analyzed. When the effect of focal males on the productivity of tester females was assessed, female body size was significant only when the productivity in the first 24 hours was taken into account. Therefore, our results in regard to the focal female productivity point out that larger females produced more offspring not only during the first 24

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hours after copulation, when the majority of the eggs are laid (Credland and Wright 1989; Zajitschek et al. 2018), but also when offspring production is measured along the entire female lifespan. This finding is in concordance with the result of a previous study carried out by Martin and Hosken (2003a), which found that, in the common dung fly, *Sepsis cynipsea*, the female LRS was positively affected by the female hind tibia length, the trait which was used as a proxy of the body size.

Female longevity affected the female LRS though the direction of the relationship between those two variables was different depending on whether LRS was measured after a single mating, or during continuous cohabitation with males. The LRS of focal females after a single copulation was negatively correlated with female longevity. This result may be related with the costs of reproduction. Reproduction generally trades-off with other biological functions, such as somatic maintenance for example (e.g. Brommer 2000; Edward and Chapman 2011). In *C. maculatus* for example, population productivity trades-off with investment on immunity that females must make to protect themselves from infections due to male-induced damage during copulation (Rönn et al. 2006; Dougherty et al. 2017 and see Messina and Fry 2003). Such kind of trade-offs have been also observed in other species of insects (Hosken 2001; Schwenke et al. 2016). In contrast to the results obtained when females were mated only once early in life, when there was continuous sexual cohabitation with harassing males, female LRS was found to be positively correlated with female longevity. This result was consistent both in the analyses of the effects of focal males on tester females, and in the analysis of responses of focal females when exposed to tester males. The reversal in the relationship between the two variables may be attributed to the direct benefits that female *C. maculatus* can obtain from multiple mating (Eady et al. 2000; Arnqvist et al. 2005 but see Rönn et al. 2006). Previous studies in *C. maculatus* have revealed that females of this species obtain nutrients and water from the ejaculates (e.g. Fox 1993; Edvardsson 2007; Ursprung et al. 2009 and see Chapter 3, 4 and 5) and that these resources could allow females to extend their lifespan, and, in addition, the resources could be allocated by females to reproduction. The formerly mentioned direct benefits of multiple mating for females may play a relevant role in our experiments because we did no provide food or water supplies to the adults, but they had to survive instead with the resources accrued during the larval phase. We maintained our beetles at aphagia; *Callosobruchus maculatus* are facultative aphagous capital breeders, and our selection lines, stock population and near-isogenic lines have always been bred at aphagia, just as the source population has always been maintained (see for instance Fox 1993; Berg and Maklakov 2012). Consequently, any additional source of nutrition and hydration results beneficial for females.

Female longevity

According to the predictions from sexual conflict, and the results by several studies comparing the evolution of both sexes under different mating systems, males are predicted to be less harmful for females, and females are predicted to be less resistant to male-induced harm, when they evolve under a monogamous mating regime because under those conditions sexual selection and sexual conflict are largely absent (e.g. Holland and Rice 1999; Gay et al. 2010; Cayetano et al. 2011). For instance, the results of seminal study carried out by Holland and Rice (1999)

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with *Drosophila melanogaster* showed that females which had evolved under monogamy (in absence of sexual conflict) died sooner than those females which had evolved under natural, polygamous conditions (in presence of sexual conflict), when they were continuously exposed to polyandrous males. However, in some cases, despite the possibility for promiscuity leads to the evolution of more harmful males, the variation in the mating system under which males evolve does not affect female survival (Crudgington et al. 2010). In our study model, the effect of multiple mating on female longevity depends on a delicate balance between the direct benefits that females may accrue from the ejaculate compounds and the direct and evident costs derived from reproduction. Unsurprisingly, the studies carried out along the last decades have found mixed results. On the one hand, an increase in the number of copulations implies not only more damage for females (Crudgington and Siva-Jothy 2000; Crudgington 2001) but also inherent costs regarding oviposition (Savalli and Fox 1999), and this lead in turn to a decrease in terms of female longevity. Additionally, lifelong cohabitation with males also has a detrimental effect on female longevity due to the costs derived from the continuous male harassment (Rönn et al. 2006; den Hollander and Gwynne 2009). However, on the contrary, multiple mating can extend the female life span under certain conditions, for example when the resources are limited (Fox 1993), due to the direct benefits such as water or nutrients that females obtain from male ejaculate (Fox 1993; Edvardsson 2007; Ursprung et al. 2009).

Our analysis revealed that the different selection regimes under which our experimental individuals evolved did not lead to divergence in baseline longevity. This means that any difference in longevity assessed when mating focal individuals, males or females, to tester individuals sourced from outside the selection experiment could be unambiguously interpreted as being the result of selection on males, or females, rather than to intrinsic differences among the lines (e.g., imagine that polygamous lines exhibited inherently lower longevities). We neither detected an effect of mating system and population spatial structure or their interaction on the longevity of females briefly exposed to males within the time elapsed for a single mating event. We only observed an interactive effect between the two formerly mentioned selection treatments affecting the longevity of tester females continuously exposed to the harassment of focal males. In non-structured populations tester females cohabiting with males which have evolved under polygamous conditions lived a little bit more than those continuously exposed to the harassment of males from the monogamous selection regimes. However, this pattern, was found to be reversed in subdivided populations. Moreover, we detected an effect of population spatial structure on the longevity of focal females exposed to continuous cohabitation with focal males, where the longevity of females from metapopulations was higher than the lifespan of the females from the undivided populations. Sexual conflict theory predicts more intense sexual conflict in larger populations, as it has been proved for our study model (Gavrilets 2000; Martin and Hosken 2003b; Gay et al. 2009; Gay et al. 2010). The lack of genetic drift, higher levels of genetic variability in large, dense populations, and higher probabilities for individuals to interact with other individuals (mates and competitors) may boost sexual antagonistic selection. Consequently, sexual conflict intensity would be attenuated at the metapopulation level, compared to populations that are not subdivided. Our results regarding the longevity of focal females continuously exposed to focal male harassment seems to

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meet this potential explanation. However, we must be cautious while interpreting our result because its significance disappeared after applying the Benjamini-Hochberg correction. Further analyses would be required to explore this possibility.

Our results of baseline longevity showed that body size explains lifespan to a large extent. In the case of females, this result was also confirmed with additional datasets: in the analyses carried when females were exposed to a unique copulation and also in the analyses after continuous exposure to male harassment, matings and mating attempts during their entire lifespan (tester females housed with focal males dataset). Probably this result may be linked to the fact that we did not supply food or water for adult beetles in our experiments. Consequently, the individuals had to survived using the resources accrued from the bean where they remained until they completed their development into adults (see Chapter 1). In that sense, those individuals which accrued a larger amount of resources from the bean, had supplies which can be conveniently allocated among the different biological functions depending on the situation, that is to say, reproduction or somatic maintenance and survival for example.

As discussed above female longevity and female LRS were significantly related but the direction of such effect was opposite when females were exposed to a single copulation than when they cohabited with several males continuously. The analysis of the female response after a single copulation showed that females that produced a lower number of adult offspring along their lifespan lived for longer. As previously mentioned, these results likely reveal the costs of reproduction (Reznick 1985; Blanckenhorn et al. 2002; Yanagi and Miyatake 2003; Rönn et al. 2006; Edward and Chapman 2011; Schwenke et al. 2016; Blacher et al. 2017). However, when female longevity was analyzed after continuous cohabitation with males, the sign of the relationship between longevity and LRS was reversed: females that produced greater numbers of offspring along their lives were the ones that live for longer. This result may be explained because even when mating implies cost for females in this species, it also provides benefits, for example, under the form of water and nutrients that may extent female lifespan (Fox 1993; Edvardsson 2007; Ursprung et al. 2009), specially when the resources are limited as it happened in our experiments where no food or water was provided along the experiment and the individuals had to survived instead with the resources accrued during the larval stages. In other words, our results suggest that the benefits of multiple mating may compensate for the costs of reproduction incurred when only oviposition without access to multiple ejaculates is allowed (see also Zajitschek et al. 2018)

Concluding remarks

The capital role of sexual selection underlying the coevolution between male and female reproductive traits has been unambiguously demonstrated in experimental evolution studies (e.g. Cayetano et al. 2011; Gay et al. 2011; Simmons and Garcia-Gonzalez 2011). To date, however, no study has tested whether the coevolution of sexual conflict adaptations and counter-adaptations follows different trajectories

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depending on spatial population structure. Here we provide the first empirical results addressing this question.

In conclusion, our results contribute significantly to the field by suggesting that:

1. The effect of the mating system is not as clear as predicted by the theories of SS and SC. Our results point out in the same direction suggested in the study of Edvardsson and Canal (2006) who suggested that there is little sexual conflict over copulation in *C. maculatus*, or it is not so intense as previously thought.

2. It seems that structure have an effect on some reproductive and behavioural traits, such as the duration of the defensive kicking behavior or the female productivity, but further analyses are required to correctly evaluate the importance of this selection treatment.

3. In this is species there are many factors affecting the outcome of the reproduction and the evaluation of the sexual conflict dynamics is complex.

4. Finally, the results yielded by our study confirm different patterns in relation to the life-history theory such as, the relationship between body size and longevity or the relationship between the longevity and the lifetime reproductive success. Moreover, our study upholds the idea that those relationships do not depend on a single factor, but instead they are the result of the interaction of multiple factors which normally are in a delicate balance (trade-offs) and may lead to different evolutionary response depending on the specific conditions under which the individuals evolve.

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Table 5.1. Initial and final sample sizes in the assays and analyses. The 'mishaps' column include the number of individuals removed from the analyses due to sample deterioration or missing data for any of the variables included in the models. LRS stands for lifetime reproductive success. Data for LRS = 0 was excluded from the analyses (see text).

Experiment	Response variable	N initial	Mishaps	LRS = 0	Influential outliers	N final
Baseline longevity	**Longevity**	960 (480 per sex)	16	-	3 (female dataset)	941 (472 males and 469 females)
Traits assayed on the first copulation	**Mating latency**	320 (160 per sex)	12 (6 per sex)	-	7 (3 from tester females and 4 from focal females datasets)	301 (151 from tester females and 150 from focal females datasets)
	Copulation duration	320 (160 per sex)	12 (6 per sex)	-	7 (3 from tester females and 4 from focal females datasets)	301 (151 from tester females and 150 from focal females datasets)
	Kicking duration	320 (160 per sex)	12 (6 per sex)	-	2 (1 from tester females and 1 from focal females datasets)	306 (153 from tester females and 153 from focal females datasets)
	Female LRS	320 (160 per sex)	12 (6 per sex)	5 (3 from tester females and 2 from focal females datasets)	5 (1 from tester females and 4 from focal females datasets)	298 (150 from tester females and 148 from focal females datasets)
	Female longevity	320 (160 per sex)	12 (6 per sex)	5 (3 from tester females and 2 from focal females datasets)	7 (5 from tester females and 2 from focal females datasets)	296 (146 from tester females and 150 from focal females datasets)
Traits assayed on the second copulation	**Mating latency**	77 focal females	-	-	1	76 focal females
	Copulation duration	77 focal females	-	-	2	75 focal females
	Kicking duration	77 focal females	-	-	3	74 focal females
Traits assayed after continuous exposure to male harassment	**Short-term productivity**	320 (160 per sex)	28	-	8 (3 from tester females and 5 focal females datasets)	284 (134 from tester females and 150 from focal females datasets)
	Female LRS	320 (160 per sex)	28	3 (2 from tester females and 1 from focal females datasets)	4 (3 from tester females and 1 from focal females datasets)	285 (132 from tester females and 153 focal females datasets)
	Female longevity	320 (160 per sex)	28	4 (3 from tester females and 1 from focal females datasets)	7 (3 from tester females and 4 from focal females datasets)	281 (131 from tester females and 150 from focal females datasets)

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Table 5.2. Analyses of baseline longevity of focal males and females. The expression 'Mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure. The degrees of freedom for the LRT are always 1 as the LRT value results from the comparison of two models (see Methods section). P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). The variance explained by the final models for focal males and focal females, respectively, are: marginal R^2= 0.09; conditional R^2= 0.21; marginal R^2= 0.07; conditional R^2= 0.14.

Sex	Effect	LRT	p
Focal Males	Mating system : structure	0.51	0.48
	Mating system	0.38	0.54
	Structure	0.001	0.98
	Elytron length	35.45	**<0.0001**
	Line (Random)	35.19	**<0.0001**
Focal Females	Mating system : structure	0.17	0.68
	Mating system	0.55	0.46
	Structure	1.18	0.28
	Elytron length	24.61	**<0.0001**
	Line (Random)	16.67	**<0.0001**

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Table 5.3. Means ± 1 SE and sample sizes (within brackets) for the measures of the baseline longevity of focal males and females for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). This measurement of longevity was carried out on virgin individuals.

Sex	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Males	17.52 ± 0.32 (119)	17.62 ± 0.30 (118)	16.88 ± 0.36 (117)	18.58 ± 0.31 (118)	17.20 ± 0.24 (236)	18.10 ± 0.22 (236)	17.57 ± 0.22 (237)	17.73 ± 0.25 (235)
Females	23.19 ± 0.45 (119)	23.46 ± 0.42 (112)	23.73 ± 0.58 (117)	25.19 ± 0.47 (121)	23.46 ± 0.36 (236)	24.36 ± 0.32 (233)	23.32 ± 0.31 (231)	24.47 ± 0.37 (238)

Table 5.4. Tukey tests pairwise comparisons of mating latency of females exposed to focal males in the selection regimes resulting from the interaction of mating system and population spatial structure at generation 47. The degrees of freedom were calculated using Satterthwaite's method.

Contrast	Estimate	SE	df	t-ratio	p
SMono- SPoly	-0.35	0.24	16.08	-1.42	0.51
SMono- NSMono	-0.41	0.24	15.66	-1.70	0.36
SMono- NSPoly	0.05	0.24	16.08	0.23	0.99
SPoly - NSMono	-0.06	0.24	14.97	-0.27	0.99
SPoly - NSPoly	0.40	0.24	15.38	1.67	0.37
NSMono- NSPoly	0.47	0.24	14.96	1.95	0.25

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Table 5.5. Analyses of female behavioural and life-history traits measured when focal males are mated to tester females for their first mating. The expression 'Mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure. The degrees of freedom for the LRT are always 1 as the LRT value results from the comparison of two models (see Methods section). P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: mating latency (marginal R^2= 0.06; conditional R^2= 0.14), copulation duration (marginal R^2= 0.15; conditional R^2= 0.15), kicking duration (marginal R^2= 0.18; conditional R^2= 0.31), female LRS (marginal R^2= 0.05; conditional R^2= 0.09), female longevity (marginal R^2= 0.09; conditional R^2= 0.09).

Response variable	Effect	LRT	p
Mating latency	Mating system : structure	4.88	0.03
	Mating system	0.09	0.76
	Structure	0.001	0.97
	Male elytron length	0.35	0.55
	Female elytron length	0.02	0.89
	Line (Random)	2.98	0.08
Copulation duration	Mating system : structure	0.13	0.72
	Mating system	6.98	**0.0082**
	Structure	6.17	**0.01**
	Male elytron length	7.68	**0.0056**
	Female elytron length	3.83	0.0502
	Line (Random)	0	1
Kicking duration	Mating system : structure	3.158	0.08
	Mating system	1.15	0.28
	Structure	2.04	0.15
	Male elytron length	15.37	**<0.0001**
	Female elytron length	15.22	**<0.0001**
	Line (Random)	9.25	**0.0024**
Female LRS	Mating system : structure	0.92	0.34
	Mating system	0.10	0.75
	Structure	0.02	0.88
	Male elytron length	6.72	0.01
	Female elytron length	1.90	0.17
	Copulation duration	0.97	0.33
	Female longevity	0.09	0.76
	Line (Random)	0.7	0.40
Female longevity	Mating system : structure	0.04	0.85
	Mating system	0.52	0.47
	Structure	0.24	0.62
	Male elytron length	0.0055	0.94
	Female elytron length	13.31	**0.0003**
	Copulation duration	0.0099	0.92
	LRS	0.0093	0.92
	Line (Random)	0	1

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Table 5.6. Means ± 1 SE and sample sizes (within brackets) for the measures of behavioural and life-history traits of females exposed to focal males (first copulation assays). The values are provided for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly).

Response variable	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Mating Latency (seconds)	124.29 ± 17.48 (35)	159.55 ± 17.03 (38)	167.38 ± 20.07 (40)	115.76 ± 15.91 (38)	147.27 ± 13.60 (75)	137.66 ± 11.85 (76)	142.64 ± 12.29 (73)	142.23 ± 13.14 (78)
Copulation Duration (seconds)	359.58 ± 11.61 (38)	392.22 ± 14.46 (37)	385.28 ± 13.41 (40)	440.56 ± 21.26 (36)	372.76 ± 8.97 (78)	416.05 ± 13.02 (73)	375.68 ± 9.38 (75)	411.46 ± 12.62 (76)
Kicking Duration (seconds)	104.47 ± 11.05 (38)	128.03 ± 12.22 (37)	130.08 ± 11.93 (40)	140.21 ± 14.50 (38)	117.60 ± 8.23 (78)	134.20 ± 9.47 (75)	116.09 ± 8.29 (75)	135.01 ± 9.30 (78)
Female LRS	53.19 ± 2.33 (37)	56.55 ± 1.93 (38)	54.15 ± 2.18 (39)	55.06 ± 2.20 (36)	53.68 ± 1.58 (76)	55.82 ± 1.45 (74)	54.89 ± 1.51 (75)	54.59 ± 1.54 (75)
Female Longevity (days)	8.19 ± 0.16 (37)	8.31 ± 0.15 (36)	8.29 ± 0.18 (38)	8.31 ± 0.21 (35)	8.24 ± 0.12 (75)	8.31 ± 0.13 (71)	8.25 ± 0.11 (73)	8.30 ± 0.14 (73)

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Table 5.7. Analyses of female behavioural and life-history traits measured when focal females are mated to tester males for their first mating. The expression 'Mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure. The degrees of freedom for the LRT are always 1 as the LRT value results from the comparison of two models (see Methods section). P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by the final model: mating latency (marginal R^2= 0.01; conditional R^2= 0.01), copulation duration (marginal R^2= 0.07; conditional R^2= 0.17), kicking duration (marginal R^2= 0.08; conditional R^2= 0.14), female LRS (marginal R^2= 0.11; conditional R^2= 0.11), female longevity (marginal R^2= 0.20; conditional R^2= 0.20).

Response variable	Effect	LRT	p
Mating latency	Mating system : structure	0.24	0.63
	Mating system	0.0004	0.98
	Structure	1.55	0.21
	Male elytron length	0.17	0.68
	Female elytron length	0.02	0.89
	Line (Random)	0.006	0.94
Copulation duration	Mating system : structure	1.11	0.29
	Mating system	2.01	0.16
	Structure	0.86	0.35
	Male elytron length	5.85	0.02
	Female elytron length	0.19	0.66
	Line (Random)	5.27	0.02
Kicking duration	Mating system : structure	0.00	0.99
	Mating system	0.01	0.91
	Structure	4.41	0.04
	Male elytron length	7.96	**0.0048**
	Female elytron length	1.75	0.09
	Line (Random)	1.75	0.19
Female LRS	Mating system : structure	1.15	0.28
	Mating system	1.88	0.17
	Structure	4.39	0.04
	Male elytron length	0.0023	0.96
	Female elytron length	2.97	0.08
	Copulation duration	0.91	0.34
	Female longevity	10.36	**0.0013**
	Line (Random)	0	1
Female longevity	Mating system : structure	0.95	0.33
	Mating system	1.91	0.17
	Structure	1.45	0.23
	Male elytron length	0.61	0.43
	Female elytron length	18.29	**<0.0001**
	Copulation duration	0.0057	0.94
	LRS	17.44	**<0.0001**
	Line (Random)	0	1

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Table 5.8. Means ± 1 SE and sample sizes (within brackets) for behavioural and life-history traits of focal females mated to tester males (first copulation assays). The values are provided for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly).

Response variable	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Mating Latency (seconds)	227.76 ± 21.77 (38)	205.05 ± 16.80 (37)	234.61 ± 20.06 (36)	242.03 ± 19.34 (39)	231.09 ± 14.75 (74)	224.03 ± 12.95 (76)	216.56 ± 13.80 (75)	238.47 ± 13.84 (75)
Copulation Duration (seconds)	332.73 ± 9.18 (40)	335.83 ± 10.15 (36)	326.00 ± 8.54 (36)	365.00 ± 12.94 (38)	329.54 ± 6.27 (76)	350.81 ± 8.40 (74)	334.20 ± 6.77 (76)	346.03 ± 8.11 (74)
Kicking Duration (seconds)	73.10 ± 7.76 (40)	80.55 ± 9.44 (38)	56.62 ± 6.98 (37)	54.68 ± 6.74 (38)	65.18 ± 5.29 (77)	67.62 ± 5.95 (76)	76.73 ± 6.06 (78)	55.64 ± 4.82 (75)
Female LRS	71.32 ± 2.25 (38)	71.05 ± 2.20 (38)	69.70 ± 2.23 (33)	63.77 ± 2.27 (39)	70.56 ± 1.58 (71)	67.36 ± 1.63 (77)	71.18 ± 1.56 (76)	66.49 ± 1.63 (72)
Female Longevity (days)	9.73 ± 0.21 (40)	9.47 ± 0.20 (38)	9.71 ± 0.29 (35)	9.41 ± 0.18 (37)	9.72 ± 0.17 (75)	9.44 ± 0.14 (75)	9.6 ± 0.15 (78)	9.56 ± 0.17 (72)

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Table 5.9. Analyses of behavioural traits measured when focal females are mated to tester males for their second mating. The expression 'Mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure. The degrees of freedom for the LRT are always 1 as the LRT value results from the comparison of two models (see Methods section). P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: mating latency (marginal R^2= 0.06; conditional R^2= 0.06), copulation duration (marginal R^2= 0.07; conditional R^2= 0.07), kicking duration (marginal R^2= 0.11; conditional R^2= 0.11).

Response variable	Effect	LRT	p
Mating latency	Mating system : structure	0.31	0.58
	Mating system	0.42	0.52
	Structure	0.83	0.36
	Female elytron length	3.81	0.0509
	Line (Random)	0	1
Copulation duration	Mating system : structure	0.43	0.51
	Mating system	1.96	0.16
	Structure	2.24	0.13
	Female elytron length	0.46	0.49
	Line (Random)	0	1
Kicking duration	Mating system : structure	3.71	0.0542
	Mating system	1.03	0.31
	Structure	8.25	**0.0041**
	Female elytron length	0.0021	0.96
	Line (Random)	0	1

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Table 5.10. Means ± 1 SE and sample sizes (within brackets) for behavioural and life-history traits of focal females mated to tester males (second copulation assays). The values are provided for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly).

Response variable	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Mating Latency (seconds)	202.67 ± 34.28 (15)	174.27 ± 19.60 (22)	235.56 ± 32.18 (27)	229.08 ± 38.07 (12)	223.81 ± 23.91 (42)	193.62 ± 18.70 (34)	185.78 ± 17.99 (37)	233.56 ± 24.90 (39)
Copulation Duration (seconds)	533.13 ± 29.00 (15)	590.35 ± 27.54 (20)	507.54 ± 18.05 (28)	533.17 ± 38.81 (12)	516.47 ± 15.42 (43)	568.91 ±22.71 (32)	565.83 ± 20.35 (35)	515.23 ± 16.99 (40)
Kicking Duration (seconds)	182.07 ± 28.31 (15)	121.48 ± 23.42 (21)	82.89 ± 11.25 (27)	85.64 ± 12.43 (11)	118.31 ± 14.29 (42)	109.16 ± 16.08 (32)	146.72 ± 18.49 (36)	83.68 ± 8.67 (38)

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Table 5.11. Analyses of tester females' short-term productivity, LRS and longevity after lifelong cohabitation with focal males. The expression 'Mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure. The degrees of freedom for the LRT are always 1 as the LRT value results from the comparison of two models (see Methods section). P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by the final models: STP (marginal R^2= 0.13; conditional R^2= 0.13), LRS (marginal R^2= 0.27; conditional R^2= 0.27), female longevity (marginal R^2= 0.34; conditional R^2= 0.34).

Response variable	Effect	LRT	p
Short-term productivity	Mating system : structure	4.93	0.03
	Mating system	1.77	0.18
	Structure	3.76	0.52
	Female elytron length	14.61	**<0.0001**
	Female longevity	2.75	0.09
	Line (Random)	0	1
Female LRS	Mating system : structure	3.05	0.08
	Mating system	3.59	0.06
	Structure	0.26	0.61
	Female elytron length	4.91	0.03
	Female longevity	24.00	**<0.0001**
	Line (Random)	0	1
Female longevity	Mating system : structure	5.79	**0.0161**
	Mating system	1.85	0.17
	Structure	1.64	0.20
	Female elytron length	7.03	**0.008**
	LRS	26.66	**<0.0001**
	Line (Random)	0	1

Table 5.12. Tukey tests pairwise comparisons of short-term productivity of tester females continuously exposed to the harassment and mating attempts of focal males in the selection regimes resulting from the interaction of mating and population spatial structure at generation 47. The degrees of freedom were calculated using Satterthwaite's method.

Contrast	Estimate	SE	df	t-ratio	p
SMono- SPoly	-234.57	85.13	135.01	-2.76	0.03
SMono- NSMono	-280.33	86.36	135.01	-3.25	0.01
SMono- NSPoly	-205.87	91.56	135.01	-2.25	0.12
SPoly - NSMono	-45.76	83.09	135.01	-0.55	0.95
SPoly - NSPoly	28.70	92.06	135.01	0.31	0.99
NSMono- NSPoly	74.46	92.74	135.01	0.80	0.85

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Table 5.13. Means ± 1 SE and sample sizes (within brackets) for the measures of short-term productivity (STP), Lifetime Reproductive Success (LRS), and longevity of tester females after lifelong exposure to the harassment and mating attempts of focal males. The values are provided for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly).

Response variable	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
STP	23.37 ±1.57 (38)	26.58 ± 1.29 (36)	27.66 ±1.04 (35)	25.92 ± 2.017 (25)	25.42 ± 0.98 (73)	26.31 ± 1.16 (61)	24.93 ± 1.03 (74)	26.93 ± 1.08 (60)
LRS	49.11 ± 3.15 (36)	52.53 ± 2.65 (36)	49.06 + 2.54 (36)	50.21 ± 3.77 (24)	49.08 ± 2.00 (72)	51.60 ± 2.17 (60)	50.82 ± 2.05 (72)	49.52 ± 2.13 (60)
Female longevity (days)	6.77 ± 0.24 (35)	5.94 ± 0.21 (36)	5.86 ± 0.19 (36)	6.21 ± 0.23 (24)	6.31 ± 0.16 (71)	6.05 ± 0.15 (60)	6.35 ± 0.16 (71)	6.00 ± 0.15 (60)

Table 5.14. Tukey tests pairwise comparisons of longevity of tester females continuously exposed to the harassment and mating attempts of focal males in the selection regimes resulting from the interaction of mating and population spatial structure at generation 47. The degrees of freedom were calculated using Satterthwaite's method.

Contrast	Estimate	SE	df	t-ratio	p
SMono- SPoly	0.69	0.26	131	2.70	0.04
SMono- NSMono	0.67	0.26	131	2.64	0.045
SMono- NSPoly	0.43	0.28	131	1.54	0.42
SPoly - NSMono	-0.02	0.25	131	-0.08	0.99
SPoly - NSPoly	-0.27	0.28	131	-0.96	0.77
NSMono- NSPoly	-0.25	0.28	131	-0.89	0.81

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Table 5.15. Analyses of focal females' short-term productivity, LRS and longevity after lifelong cohabitation with standardized tester males. The expression 'Mating system : structure' refers to the selection regimes resulting from the interaction between mating system and population spatial structure. The degrees of freedom for the LRT are always 1 as the LRT value results from the comparison of two models (see Methods section). P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by the final models: STP (marginal R^2= 0.15; conditional R^2= 0.18), LRS marginal R^2= 0.35; conditional R^2= 0.37), female longevity (marginal R^2= 0.15; conditional R^2= 0.15).

Response variable	Effect	LRT	p
Short-term productivity	Mating system : structure	0.42	0.51
	Mating system	0.42	0.12
	Structure	1.27	0.26
	Female elytron length	17.11	**<0.0001**
	Female longevity	0.52	0.47
	Line (Random)	0.67	0.41
Female LRS	Mating system : structure	0.85	0.36
	Mating system	3.15	0.08
	Structure	0.84	0.36
	Female elytron length	30.92	**<0.0001**
	Female longevity	18.69	**<0.0001**
	Line (Random)	0.25	0.62
Female longevity	Mating system : structure	0.17	0.68
	Mating system	0.02	0.89
	Structure	5.74	0.02
	Female elytron length	2.28	0.13
	LRS	16.09	**<0.0001**
	Line (Random)	0	1

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Table 5.16. Means ± 1 SE and sample sizes (within brackets) for the measures of short-term productivity (STP), Lifetime Reproductive Success (LRS), and longevity of focal females after lifelong exposure to tester males. The values are provided for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly).

Response variable	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
STP	32.63 ± 1.04 (38)	34.61 ± 0.84 (36)	32.97 ± 0.93 (37)	35.28 ± 0.82 (39)	32.80 ± 0.69 (75)	34.96 ± 0.59 (75)	33.59 ± 0.68 (74)	34.16 ± 0.63 (76)
LRS	69.11 ± 2.54 (38)	74.95 ± 2.37 (38)	66.61 ± 2.42 (38)	73.97 ± 2.00 (39)	67.86 ± 1.75 (76)	74.45 ± 1.54 (77)	72.03 ± 1.76 (76)	70.34 ± 1.61 (77)
Female longevity (days)	6.74 ± 0.19 (35)	6.89 ± 0.12 (38)	6.35 ± 0.17 (37)	6.43 ± 0.16 (40)	6.54 ± 0.13 (72)	6.65 ± 0.10 (78)	6.82 ± 0.11 (73)	6.39 ± 0.11 (77)

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Appendix Chapter 5

Model: Evolution of male and female baseline longevity

Males

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]
Formula: longev ~ ss + structure + ss:structure + centelytrum + (1 | line)
   Data: data
     AIC      BIC   logLik deviance df.resid
  2487.9   2517.0  -1237.0   2473.9      465
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.48192 -0.72607 -0.01023  0.70983  2.98207
Random effects:
 Groups   Name        Variance Std.Dev.

 line     (Intercept)  1.448   1.204
 Residual             10.469   3.236
Number of obs: 472, groups:  line, 16
Fixed effects:
                       Estimate Std. Error        df t value Pr(>|t|)
(Intercept)            18.66084    0.69752  18.00000  26.753 4.44e-16 ***
sspoly                 -0.05177    0.94956  15.60000  -0.055    0.957
structurenometa        -0.49813    0.94998  15.60000  -0.524    0.607
centelytrum            13.78628    2.28852 466.90000   6.024 3.45e-09 ***
sspoly:structurenometa   0.96653    1.34743  15.80000   0.717    0.484
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: longev ~ ss + structure + centelytrum + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2486.4   2511.4  -1237.2   2474.4      466
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.49671 -0.72688 -0.01187  0.71994  2.96780
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)  1.513   1.230
 Residual             10.468   3.235
Number of obs: 472, groups:  line, 16
Fixed effects:
                 Estimate Std. Error       df t value Pr(>|t|)
(Intercept)      18.4353     0.6303  19.9000  29.248  < 2e-16 ***
sspoly            0.4253     0.6882  16.1000   0.618    0.545
structurenometa  -0.0169     0.6840  15.8000  -0.025    0.981
centelytrum      13.9521     2.2831 464.3000   6.111  2.1e-09 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Females

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: longev ~ ss + structure + ss:structure + centelytrum + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2845.8   2874.8  -1415.9   2831.8      462
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.76342 -0.67311 -0.02051  0.72621  2.87310
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)  1.872   1.368
 Residual             23.547   4.853
Number of obs: 469, groups:  line, 16
Fixed effects:
                       Estimate Std. Error       df t value Pr(>|t|)
(Intercept)             22.1675     0.8413  17.6000  26.348 1.33e-15 ***
sspoly                   0.2722     1.1605  16.0000   0.235    0.817
structurenometa          0.5701     1.1556  15.8000   0.493    0.629
centelytrum             15.9295     3.1601 448.7000   5.041 6.74e-07 ***
sspoly:structurenometa   0.6843     1.6401  16.0000   0.417    0.682
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: longev ~ ss + structure + centelytrum + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2843.9   2868.8  -1416.0   2831.9      463
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.77468 -0.66337 -0.02067  0.71686  2.86220
```


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```
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)  1.90    1.378
 Residual             23.55    4.853
Number of obs: 469, groups:  line, 16
Fixed effects:
                 Estimate Std. Error       df t value Pr(>|t|)
(Intercept)      21.9932     0.7330  17.7000  30.004  < 2e-16 ***
sspoly            0.6151     0.8242  16.0000   0.746    0.466
structurenometa   0.9101     0.8236  15.9000   1.105    0.286
centelytrum      16.0045     3.1548 445.7000   5.073 5.75e-07 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Analyses of female behavioural and life-history traits measured when focal males are mated to tester females for their first mating.

Mating latency

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llatency ~ ss + structure + ss:structure + centfel + centmel + (1|line)
     AIC      BIC   logLik deviance df.resid
   374.6    398.7   -179.3    358.6      143
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.4140 -0.5952  0.1030  0.6079  2.1098
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.05603  0.2367
 Residual             0.58792  0.7668
Number of obs: 151, groups:  line, 16
Fixed effects:
                        Estimate Std. Error        df t value Pr(>|t|)
(Intercept)              4.47441    0.17963  17.72000  24.908 3.11e-15 ***
sspoly                   0.34853    0.25160  17.16000   1.385   0.1837
structurenometa          0.39660    0.24850  16.28000   1.596   0.1297
centfel                 -0.06497    0.64015 140.46000  -0.101   0.9193
centmel                 -0.53844    0.90350 147.58000  -0.596   0.5521
sspoly:structurenometa  -0.77728    0.35130  16.21000  -2.213   0.0416 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llatency ~ ss + structure + ss:structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
   370.9    389.0   -179.5    358.9      145
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.4014 -0.6058  0.1217  0.6766  2.0947
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.05273  0.2296
 Residual             0.59127  0.7689
Number of obs: 151, groups:  line, 16
Fixed effects:
                       Estimate Std. Error      df t value Pr(>|t|)
(Intercept)              4.4777     0.1739 16.7910  25.748 6.22e-15 ***
sspoly                   0.3451     0.2429 16.0820   1.421   0.1745
structurenometa          0.4088     0.2413 15.6620   1.695   0.1099
sspoly:structurenometa  -0.8104     0.3402 15.5190  -2.382   0.0304 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Copulation duration

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom ['lmerMod']. Formula: Lcopdur ~ ss+structure+ss:structure+centfel+centmel + (1|line)
     AIC      BIC   logLik deviance df.resid
   -26.1     -1.9     21.0    -42.1      143
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.49326 -0.69373  0.00206  0.58337  2.89914
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 4.281e-16 2.069e-08
 Residual             4.432e-02 2.105e-01
Number of obs: 151, groups:  line, 16
Fixed effects:
                        Estimate Std. Error        df t value Pr(>|t|)
(Intercept)              5.84843    0.03581 151.00000 163.321  < 2e-16 ***
sspoly                   0.11498    0.05088 151.00000   2.260  0.02527 *
structurenometa          0.10492    0.04932 151.00000   2.127  0.03502 *
centfel                 -0.34689    0.17341 151.00000  -2.000  0.04725 *
centmel                  0.65693    0.22807 151.00000   2.880  0.00455 **
sspoly:structurenometa  -0.02582    0.07088 151.00000  -0.364  0.71610
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
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Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom ['lmerMod']. Formula: Lcopdur ~ ss + structure + centfel + centmel + (1 | line)
     AIC      BIC   logLik deviance df.resid
   -27.9     -6.8     21.0    -41.9      144
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.53387 -0.69449  0.01304  0.59977  2.91804
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 8.651e-21 9.301e-11
 Residual             4.436e-02 2.106e-01
Number of obs: 151, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)       5.85487    0.03115 151.00000 187.970  < 2e-16 ***
sspoly            0.10212    0.03666 151.00000   2.785  0.00603 **
structurenometa   0.09225    0.03498 151.00000   2.637  0.00923 **
centfel          -0.33961    0.17233 151.00000  -1.971  0.05059 .
centmel           0.63789    0.22211 151.00000   2.872  0.00467 **
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Kicking duration

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lkicklen ~ ss + structure + ss:structure + centfel +centmel+ (1 | line)
     AIC      BIC   logLik deviance df.resid
   289.1    313.3   -136.5    273.1      145
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.2707 -0.6281  0.1076  0.6655  2.6192
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.04015  0.2004
 Residual             0.32140  0.5669
Number of obs: 153, groups:  line, 16
Fixed effects:
                      Estimate Std. Error       df t value Pr(>|t|)
(Intercept)             4.3099     0.1391  16.5500  30.978 4.44e-16 ***
sspoly                  0.4289     0.1972  16.7000   2.175   0.0443 *
structurenometa         0.4866     0.1944  15.7500   2.503   0.0237 *
centfel                -1.9404     0.4681 141.2900  -4.145 5.82e-05 ***
centmel                 2.8893     0.6559 152.3900   4.405 1.99e-05 ***
sspoly:structurenometa -0.5225     0.2763  16.0100  -1.891   0.0769 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lkicklen ~ ss + structure + centfel + centmel + (1 | line)
     AIC      BIC   logLik deviance df.resid
   290.3    311.5   -138.1    276.3      146
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.3022 -0.5583  0.0779  0.6985  2.5905
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.05858  0.2420
 Residual             0.32049  0.5661
Number of obs: 153, groups:  line, 16
Fixed effects:
                 Estimate Std. Error       df t value Pr(>|t|)
(Intercept)       4.4407     0.1341  17.0000  33.118  < 2e-16 ***
sspoly            0.1695     0.1557  17.3500   1.088    0.291
structurenometa   0.2256     0.1529  16.1900   1.476    0.159
centfel          -1.8772     0.4670 142.3100  -4.020 9.41e-05 ***
centmel           2.6510     0.6562 152.6100   4.040 8.46e-05 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Female LRS

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: LRS2 ~ ss + structure + ss:structure + centfel + centmel + centcopdur +
centlongev + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2601.3   2631.4  -1290.6   2581.3      140
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.24993 -0.70646 -0.07429  0.77006  2.33094
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)   68527   261.8
 Residual             1683239  1297.4
Number of obs: 150, groups:  line, 16
```


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```
Fixed effects:
                          Estimate Std. Error        df t value Pr(>|t|)
(Intercept)             3152.2248   261.6587   18.2700  12.047 3.94e-10 ***
sspoly                   140.9376   369.2433   18.1400   0.382  0.70712
structurenometa           79.2293   361.0292   16.5500   0.219  0.82898
centfel                 1611.5472  1120.7868  163.3700   1.438  0.15238
centmel                 3906.6767  1466.1839  153.6200   2.665  0.00853 **
centcopdur                 0.5766     0.5926  167.2300   0.973  0.33198
centlongev               -67.5562    98.3481  169.7800  -0.687  0.49308
sspoly:structurenometa -384.8001   511.2923   16.4700  -0.753  0.46231
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: LRS2 ~ ss + structure + centmel + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2597.2   2615.3  -1292.6   2585.2      144
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.23611 -0.62478 -0.01815  0.70467  2.20356
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)   66604   258.1
 Residual             1730869  1315.6
Number of obs: 150, groups:  line, 16
Fixed effects:
                Estimate Std. Error      df t value Pr(>|t|)
(Intercept)      3147.47     219.34   15.78  14.350  1.8e-10 ***
sspoly             82.86     254.68   15.93   0.325  0.74917
structurenometa   -37.92     250.95   15.30  -0.151  0.88187
centmel          3861.36    1449.45  134.70   2.664  0.00866 **
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Female longevity

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llongev ~ ss + structure + ss:structure + centfel + centmel +
centcopdur + centLRS + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -214.5   -184.7    117.3   -234.5      136
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.69652 -0.49632 -0.05993  0.67875  2.41291
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.00000  0.0000
 Residual             0.01175  0.1084
Number of obs: 146, groups:  line, 16
Fixed effects:
                         Estimate Std. Error         df t value Pr(>|t|)
(Intercept)             2.234e+00  1.891e-02  1.460e+02 118.168  < 2e-16 ***
sspoly                 -1.757e-02  2.717e-02  1.460e+02  -0.647 0.518912
structurenometa        -1.293e-02  2.601e-02  1.460e+02  -0.497 0.619788
centfel                 3.357e-01  9.028e-02  1.460e+02   3.719 0.000285 ***
centmel                -1.326e-02  1.232e-01  1.460e+02  -0.108 0.914421
centcopdur              5.963e-06  4.930e-05  1.460e+02   0.121 0.903901
centLRS                -5.020e-05  7.065e-04  1.460e+02  -0.071 0.943450
sspoly:structurenometa  7.559e-03  3.712e-02  1.460e+02   0.204 0.838915
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llongev ~ ss + structure + centfel + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -222.4   -204.5    117.2   -234.4      140
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.68138 -0.50359 -0.06164  0.65590  2.40069
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.00000  0.0000
 Residual             0.01175  0.1084
Number of obs: 146, groups:  line, 16
Fixed effects:
                Estimate Std. Error        df t value Pr(>|t|)
(Intercept)      2.23205    0.01610 146.00000 138.646  < 2e-16 ***
sspoly          -0.01363    0.01884 146.00000  -0.724 0.470374
structurenometa -0.00901    0.01825 146.00000  -0.494 0.622172
centfel          0.33233    0.08903 146.00000   3.733 0.000271 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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Model: Analyses of female behavioural and life-history traits measured when focal females are mated to tester males for their first mating.
Mating latency
Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llatency ~ ss + structure + ss:structure + centfel+centmel + (1 | line)
     AIC      BIC   logLik deviance df.resid
   260.4    284.5   -122.2    244.4      142
Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.3810 -0.7193 -0.0176  0.7614  2.0663
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 0.0001494 0.01222
 Residual             0.2985668 0.54641
Number of obs: 150, groups:  line, 16
Fixed effects:
                       Estimate Std. Error        df t value Pr(>|t|)
(Intercept)             5.24851    0.09360  18.18000  56.071   <2e-16 ***
sspoly                 -0.03397    0.14351  23.20000  -0.237    0.815
structurenometa         0.07874    0.12868  16.77000   0.612    0.549
centfel                 0.01840    0.48194 142.31000   0.038    0.970
centmel                -0.20777    0.56128 144.06000  -0.370    0.712
sspoly:structurenometa  0.08022    0.18144  16.48000   0.442    0.664
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llatency ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
   254.8    269.9   -122.4    244.8      145
Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.3799 -0.7090  0.0137  0.7636  2.0495
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000916 0.03027
 Residual             0.298563 0.54641
Number of obs: 150, groups:  line, 16
Fixed effects:
                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)      5.232497   0.078055 15.506000  67.036   <2e-16 ***
sspoly           0.001837   0.090547 15.758000   0.020    0.984
structurenometa  0.116134   0.090540 15.747000   1.283    0.218
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Copulation duration
Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lcopdur ~ ss + structure + ss:structure + centfel + centmel +(1 | line)
     AIC      BIC   logLik deviance df.resid
   -96.1    -72.0     56.1   -112.1      142
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.49407 -0.66375 -0.04777  0.50950  2.64071
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.002932 0.05415
 Residual             0.025657 0.16018
Number of obs: 150, groups:  line, 16
Fixed effects:
                        Estimate Std. Error         df t value Pr(>|t|)
(Intercept)              5.793365   0.038298  16.850000 151.270   <2e-16 ***
sspoly                   0.003549   0.057949  21.280000   0.061   0.9517
structurenometa         -0.004259   0.053435  16.150000  -0.080   0.9374
centfel                 -0.087909   0.150096 149.950000  -0.586   0.5590
centmel                 -0.403909   0.168903 140.570000  -2.391   0.0181 *
sspoly:structurenometa   0.086840   0.076324  16.700000   1.138   0.2713
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lcopdur ~ ss + structure + centmel + (1 | line)
     AIC      BIC   logLik deviance df.resid
   -98.7    -80.6     55.3   -110.7      144
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.46386 -0.67655 -0.07011  0.51794  2.59286

Random effects:
 Groups   Name        Variance Std.Dev.
```


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```
 line     (Intercept) 0.00328  0.05727
 Residual             0.02575  0.16046
Number of obs: 150, groups:  line, 16
Fixed effects:
                  Estimate Std. Error        df t value Pr(>|t|)
(Intercept)        5.76835    0.03336  15.25000 172.919   <2e-16 ***
sspoly             0.05707    0.03887  15.82000   1.468   0.1617
structurenometa    0.03660    0.03893  15.91000   0.940   0.3612
centmel           -0.41253    0.16856 141.71000  -2.447   0.0156 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Kicking duration
Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lkicklen ~ ss + structure + ss:structure + centfel + centmel+(1 | line)
     AIC      BIC   logLik deviance df.resid
   336.0    360.3   -160.0    320.0      145
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.35525 -0.73295  0.05624  0.64668  2.25260
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.02149  0.1466
 Residual             0.45608  0.6753
Number of obs: 153, groups:  line, 16
Fixed effects:
                       Estimate Std. Error       df t value Pr(>|t|)
(Intercept)              4.1820     0.1352  17.8700  30.941  < 2e-16 ***
sspoly                  -0.1655     0.2051  22.5600  -0.807  0.42830
structurenometa         -0.3157     0.1872  16.7400  -1.686  0.11032
centfel                 -1.0446     0.6103 152.0300  -1.712  0.08899 .
centmel                  1.9099     0.6966 144.9900   2.742  0.00688 **
sspoly:structurenometa   0.0620     0.2665  17.0400   0.233  0.81878
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lkicklen ~ ss + structure + centmel + (1 | line)
     AIC      BIC   logLik deviance df.resid
   334.9    353.1   -161.4    322.9      147
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.4412 -0.6328  0.1016  0.7203  2.2465
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.02776  0.1666
 Residual             0.46064  0.6787
Number of obs: 153, groups:  line, 16
Fixed effects:
                  Estimate Std. Error        df t value Pr(>|t|)
(Intercept)        4.12066    0.11861  16.09000  34.740  < 2e-16 ***
sspoly            -0.01544    0.13801  16.56000  -0.112  0.91229
structurenometa   -0.31202    0.13851  16.77000  -2.253  0.03797 *
centmel            1.99266    0.69670 145.92000   2.860  0.00486 **
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Female LRS
Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: LRS2 ~ ss + structure + ss:structure + centfel + centmel + centcopdur +
centlongev + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2641.2   2671.2  -1310.6   2621.2      138
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.18626 -0.72227  0.08792  0.68274  2.83852
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)        0       0
 Residual             2878864    1697
Number of obs: 148, groups:  line, 16
Fixed effects:
                       Estimate Std. Error       df t value Pr(>|t|)
(Intercept)            5109.946    297.055  163.640  17.202  < 2e-16 ***
sspoly                  312.450    455.011  163.640   0.687 0.493252
structurenometa        -309.568    410.438  163.640  -0.754 0.451791
centfel                3228.092   1677.076  163.640   1.925 0.055985 .
centmel                 233.876   1802.360  163.640   0.130 0.896915
centcopdur                2.055      1.913  163.640   1.074 0.284320
centlongev             -396.193    106.901  163.640  -3.706 0.000288 ***
sspoly:structurenometa -790.455    568.943  163.640  -1.389 0.166617
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: LRS2 ~ ss + structure + centlongev + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2639.1   2657.1  -1313.5   2627.1      142
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.41058 -0.74245 -0.00304  0.80164  2.94264
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)        0       0
 Residual             2995539  1731
Number of obs: 148, groups:  line, 16
Fixed effects:
                Estimate Std. Error     df t value Pr(>|t|)
(Intercept)       5413.6      244.6  170.3  22.136  < 2e-16 ***
sspoly            -391.7      285.0  170.3  -1.374  0.17112
structurenometa   -602.2      285.0  170.3  -2.113  0.03606 *
centlongev        -329.8      100.7  170.3  -3.277  0.00127 **
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Female longevity

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llongev ~ ss + structure + ss:structure + centfel + centmel +
centcopdur + centLRS + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -212.6   -182.5    116.3   -232.6      140
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.2465 -0.5620  0.0257  0.5914  3.0929
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.00000  0.0000
 Residual             0.01242  0.1114
Number of obs: 150, groups:  line, 16
Fixed effects:
                        Estimate Std. Error         df t value Pr(>|t|)
(Intercept)             2.341e+00  1.890e-02  1.500e+02 123.857  < 2e-16 ***
sspoly                  4.759e-02  2.931e-02  1.500e+02   1.624    0.107
structurenometa        -7.540e-03  2.614e-02  1.500e+02  -0.288    0.773
centfel                 4.561e-01  9.980e-02  1.500e+02   4.570 1.01e-05 ***
centmel                 8.362e-02  1.166e-01  1.500e+02   0.717    0.474
centcopdur              1.605e-05  1.260e-04  1.500e+02   0.127    0.899
centLRS                -2.527e-03  5.838e-04  1.500e+02  -4.328 2.74e-05 ***
sspoly:structurenometa -3.425e-02  3.726e-02  1.500e+02  -0.919    0.359
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llongev ~ ss + structure + centfel + centLRS + (1 | line)
     AIC      BIC   logLik deviance df.resid
  -217.1   -196.1    115.6   -231.1      143
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.2103 -0.5501  0.0176  0.5798  3.1778
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.00000  0.000
 Residual             0.01254  0.112
Number of obs: 150, groups:  line, 16
Fixed effects:
                  Estimate Std. Error         df t value Pr(>|t|)
(Intercept)      2.348e+00  1.623e-02  1.500e+02 144.674  < 2e-16 ***
sspoly           3.000e-02  2.163e-02  1.500e+02   1.387    0.168
structurenometa -2.236e-02  1.854e-02  1.500e+02  -1.206    0.230
centfel          4.353e-01  9.870e-02  1.500e+02   4.411 1.96e-05 ***
centLRS         -2.504e-03  5.822e-04  1.500e+02  -4.301 3.05e-05 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Analyses of behavioural traits measured when focal females are mated to tester males for their second mating.

Mating latency

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llatency ~ ss + structure + ss:structure + centfel + (1 | line)
     AIC      BIC   logLik deviance df.resid
   175.0    191.3    -80.5    161.0       69
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.6448 -0.6450  0.1829  0.7299  1.7319
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.0000   0.0000
 Residual             0.4868   0.6977
Number of obs: 76, groups:  line, 15
```


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FRANCISCO GARCIA GONZALEZ 31/05/2018 09:21:50
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```
Fixed effects:
                         Estimate Std. Error       df t value Pr(>|t|)
(Intercept)               5.07846    0.18092 76.00000  28.070   <2e-16 ***
sspoly                   -0.09388    0.23384 76.00000  -0.401   0.6892
structurenometa           0.17235    0.23157 76.00000   0.744   0.4590
centfel                   2.05293    1.08160 76.00000   1.898   0.0615 .
sspoly:structurenometa -0.04331    0.35833 76.00000  -0.121   0.9041
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Llatency ~ ss + structure + centfel + (1 | line)
     AIC      BIC   logLik deviance df.resid
   173.0    187.0    -80.5    161.0       70
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.6305 -0.6540  0.1951  0.7387  1.7419
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 1.955e-16 1.398e-08
 Residual             4.869e-01 6.978e-01
Number of obs: 76, groups:  line, 15
Fixed effects:
                 Estimate Std. Error      df t value Pr(>|t|)
(Intercept)       5.0901     0.1532 76.0000  33.230   <2e-16 ***
sspoly           -0.1127     0.1745 76.0000  -0.646   0.5202
structurenometa   0.1530     0.1673 76.0000   0.915   0.3632
centfel           2.0079     1.0156 76.0000   1.977   0.0517 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Copulation duration

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lcopdur ~ ss + structure + ss:structure + centfel + (1 | line)
     AIC      BIC   logLik deviance df.resid
   -10.8      5.4     12.4    -24.8       68
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.62765 -0.63645  0.02641  0.70648  1.96988
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.00000  0.000
 Residual             0.04204  0.205
Number of obs: 75, groups:  line, 15
Fixed effects:
                         Estimate Std. Error       df t value Pr(>|t|)
(Intercept)               6.26225    0.05315 75.00000 117.812   <2e-16 ***
sspoly                    0.10087    0.07014 75.00000   1.438    0.155
structurenometa          -0.05488    0.06800 75.00000  -0.807    0.422
centfel                  -0.14728    0.30914 75.00000  -0.476    0.635
sspoly:structurenometa -0.04708    0.10660 75.00000  -0.442    0.660
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lcopdur ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
   -14.2     -2.6     12.1    -24.2       70
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.57565 -0.59870  0.07272  0.67995  2.06004
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.00000  0.0000
 Residual             0.04241  0.2059
Number of obs: 75, groups:  line, 15
Fixed effects:
                 Estimate Std. Error       df t value Pr(>|t|)
(Intercept)       6.27844    0.04503 75.00000 139.428   <2e-16 ***
sspoly            0.07040    0.04999 75.00000   1.408    0.163
structurenometa -0.07470    0.04956 75.00000  -1.507    0.136
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Kicking duration

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lkicklen ~ ss + structure + ss:structure + centfel + (1 | line)
     AIC      BIC   logLik deviance df.resid
   170.3    186.5    -78.2    156.3       67
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.16921 -0.77838  0.00464  0.67806  2.34949
```


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```
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.0000   0.0000
 Residual             0.4843   0.6959
Number of obs: 74, groups:  line, 15
Fixed effects:
                       Estimate Std. Error      df t value Pr(>|t|)
(Intercept)              5.0147     0.1804 74.0000  27.795  < 2e-16 ***
sspoly                  -0.5022     0.2354 74.0000  -2.134 0.036198 *
structurenometa         -0.8705     0.2334 74.0000  -3.730 0.000372 ***
centfel                 -0.8684     1.0618 74.0000  -0.818 0.416103
sspoly:structurenometa   0.7805     0.3678 74.0000   2.122 0.037190 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Lkicklen ~ ss + structure + (1 | line)
     AIC      BIC   logLik deviance df.resid
   170.7    182.2    -80.4    160.7       69
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.28995 -0.78959 -0.01544  0.83170  2.06933
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.0000   0.0000
 Residual             0.5137   0.7168
Number of obs: 74, groups:  line, 15
Fixed effects:
                 Estimate Std. Error      df t value Pr(>|t|)
(Intercept)        4.8168     0.1576 74.0000  30.572   <2e-16 ***
sspoly            -0.1797     0.1761 74.0000  -1.020   0.3109
structurenometa   -0.5301     0.1746 74.0000  -3.037   0.0033 **
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model: Analyses of tester female short-term productivity, LRS and longevity after lifelong cohabitation with focal males.
Short-term productivity

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom ['lmerMod']. Formula: Sadults.first.day.vial ~ ss + structure + ss:structure + centfel +
centlongev.setup + (1 | line)
     AIC      BIC   logLik deviance df.resid
  1966.1   1989.3   -975.1   1950.1      126
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.47720 -0.45438  0.05809  0.66621  2.73703
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)        0      0.0
 Residual             122425   349.9
Number of obs: 134, groups:  line, 16
Fixed effects:
                       Estimate Std. Error      df t value Pr(>|t|)
(Intercept)              602.04      57.75  135.01  10.426  < 2e-16 ***
sspoly                   234.57      85.13  135.01   2.756  0.00667 **
structurenometa          280.33      86.36  135.01   3.246  0.00148 **
centfel                 1067.84     349.52  135.01   3.055  0.00271 **
centlongev.setup          40.36      24.21  135.01   1.667  0.09787 .
sspoly:structurenometa  -309.03     128.43  135.01  -2.406  0.01747 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom ['lmerMod']. Formula: Sadults.first.day.vial ~ ss+structure+ss:structure+centfel+ (1 |line)
     AIC      BIC   logLik deviance df.resid
  1966.9   1987.2   -976.4   1952.9      127
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.38862 -0.51465  0.04854  0.64585  2.60303
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)        0      0.0
 Residual             124963   353.5
Number of obs: 134, groups:  line, 16
Fixed effects:
                       Estimate Std. Error      df t value Pr(>|t|)
(Intercept)              617.78      57.56  133.54  10.734  < 2e-16 ***
sspoly                   215.42      85.22  133.54   2.528 0.012639 *
structurenometa          257.35      86.14  133.54   2.988 0.003346 **
centfel                 1286.29     327.36  133.54   3.929 0.000136 ***
sspoly:structurenometa  -289.44     129.21  133.54  -2.240 0.026735 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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Long-term productivity
Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: SLRS ~ ss + structure + ss:structure + centfel + centlongev.setup +
(1 | line)
     AIC      BIC   logLik deviance df.resid
  2287.1   2310.1  -1135.5   2271.1      124
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.91116 -0.72261  0.06518  0.76712  2.19592
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)       0     0
 Residual            1736337  1318
Number of obs: 132, groups:  line, 16
Fixed effects:
                        Estimate Std. Error      df t value Pr(>|t|)
(Intercept)              2525.55     222.29  157.92  11.362  < 2e-16 ***
sspoly                    841.97     322.78  157.92   2.608  0.00997 **
structurenometa           512.60     323.90  157.92   1.583  0.11552
centfel                  3400.90    1315.22  157.92   2.586  0.01062 *
centlongev.setup          486.08      91.56  157.92   5.309 3.69e-07 ***
sspoly:structurenometa  -849.79     484.18  157.92  -1.755  0.08118 .
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
  degrees of freedom [lmerMod]. Formula: SLRS ~ ss + structure + centfel+centlongev.setup +(1|line)
     AIC      BIC   logLik deviance df.resid
  2288.1   2308.3  -1137.1   2274.1      125
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.93681 -0.60414  0.04805  0.72222  2.32801
Random effects:
 Groups   Name        Variance  Std.Dev.
 line     (Intercept) 1.196e-12 1.094e-06
 Residual             1.777e+06 1.333e+03
Number of obs: 132, groups:  line, 16
Fixed effects:
                  Estimate Std. Error      df t value Pr(>|t|)
(Intercept)        2710.68     197.94  141.40  13.695  < 2e-16 ***
sspoly              451.00     236.31  141.40   1.909   0.0584 .
structurenometa     120.42     237.20  141.40   0.508   0.6125
centfel            2906.47    1299.60  141.40   2.236   0.0269 *
centlongev.setup    473.79      92.35  141.40   5.130 9.37e-07 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Female longevity
Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: longev.setup ~ ss+structure+ss:structure+centfel+centLRS + (1 | line)
     AIC      BIC   logLik deviance df.resid
   398.1    421.1   -191.0    382.1      123
Scaled residuals:
     Min       1Q   Median       3Q      Max
-3.15874 -0.57506  0.07099  0.59737  3.02115
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.000    0.00
 Residual             1.082    1.04
Number of obs: 131, groups:  line, 16
Fixed effects:
                         Estimate Std. Error         df t value Pr(>|t|)
(Intercept)              7.009478   0.183933 131.000000  38.109  < 2e-16 ***
sspoly                  -0.693001   0.256434 131.000000  -2.702  0.00780 **
structurenometa         -0.673109   0.255140 131.000000  -2.638  0.00934 **
centfel                  2.759447   1.026674 131.000000   2.688  0.00813 **
centLRS                  0.029420   0.005411 131.000000   5.437 2.56e-07 ***
sspoly:structurenometa   0.940401   0.386450 131.000000   2.433  0.01630 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model: Values identical to full model.

Model: Analyses of focal female short-term productivity, LRS and longevity after lifelong cohabitation with tester males.
Short-term productivity
Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: Sadults.first.day.vial ~ ss + structure + ss:structure + centfel +
centlongev.setup + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2191.0   2215.1  -1087.5   2175.0      142
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.5258 -0.6695 -0.1120  0.5763  2.6215
Random effects:
```


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```
 Groups   Name        Variance Std.Dev.
 line     (Intercept)   3370    58.06
 Residual             113118   336.33
Number of obs: 150, groups:  line, 16
Fixed effects:
                      Estimate Std. Error      df t value Pr(>|t|)
(Intercept)            1036.02      63.88   17.54  16.219 5.31e-12 ***
sspoly                  154.77      89.30   17.08   1.733    0.101
structurenometa         118.77      91.10   17.96   1.304    0.209
centfel                1669.87     379.51  129.12   4.400 2.24e-05 ***
centlongev.setup        -22.43      27.85  149.77  -0.805    0.422
sspoly:structurenometa  -95.68     128.03   17.65  -0.747    0.465
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations todegrees of
freedom [lmerMod]. Formula: Sadults.first.day.vial ~ ss + structure + centfel + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2188.1   2206.2  -1088.1   2176.1      144
Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.46848 -0.68971 -0.07168  0.59309  2.64610
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)   4108    64.09
 Residual             113367   336.70
Number of obs: 150, groups:  line, 16
Fixed effects:
                 Estimate Std. Error      df t value Pr(>|t|)
(Intercept)      1057.51      55.72   16.63  18.979 1.06e-12 ***
sspoly            103.99      64.08   16.38   1.623    0.124
structurenometa    74.03      64.49   16.76   1.148    0.267
centfel          1533.35     358.39  119.99   4.278 3.81e-05 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Long-term productivity

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: SLRS ~ ss+structure+ss:structure+centfel+centlongev.setup+(1 | line)
     AIC      BIC   logLik deviance df.resid
  2706.4   2730.6  -1345.2   2690.4      145
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.6661 -0.7283  0.0310  0.6732  2.2626
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)   48380   220
 Residual             2491363  1578
Number of obs: 153, groups:  line, 16
Fixed effects:
                      Estimate Std. Error       df t value Pr(>|t|)
(Intercept)            4449.78     288.47    17.31  15.425 1.49e-11 ***
sspoly                  763.19     398.62    16.05   1.915 0.073547 .
structurenometa         468.66     410.00    17.44   1.143 0.268459
centfel                10356.24    1756.19   118.53   5.897 3.57e-08 ***
centlongev.setup         502.96     128.28   140.13   3.921 0.000138 ***
sspoly:structurenometa  -480.85     572.30    16.64  -0.840 0.412705
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: SLRS ~ ss + structure + centfel + centlongev.setup + (1 | line)
     AIC      BIC   logLik deviance df.resid
  2705.1   2726.3  -1345.5   2691.1      146
Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.5933 -0.6972  0.0263  0.6548  2.1901
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept)   57805   240.4
 Residual             2494977  1579.5
Number of obs: 153, groups:  line, 16
Fixed effects:
                 Estimate Std. Error       df t value Pr(>|t|)
(Intercept)       4575.82     249.52    16.26  18.338 2.72e-12 ***
sspoly             524.75     285.77    15.68   1.836   0.0853 .
structurenometa    221.79     288.65    16.29   0.768   0.4533
centfel          10050.64    1716.11   108.56   5.857 5.11e-08 ***
centlongev.setup   514.20     127.77   140.83   4.024 9.29e-05 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Female longevity

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: longev.setup ~ss+structure+ss:structure+centfel+centLRS + (1 | line)
```


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```
     AIC      BIC   logLik deviance df.resid
   408.5    432.6   -196.3    392.5      142
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.3838 -0.6871 -0.0223  0.6280  2.1120
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.0000   0.0000
 Residual             0.8016   0.8953
Number of obs: 150, groups:  line, 16
Fixed effects:
                      Estimate Std. Error         df t value Pr(>|t|)
(Intercept)           6.449657   0.164779 150.000000  39.141  < 2e-16 ***
sspoly                0.129321   0.212197 150.000000   0.609  0.54316
structurenometa      -0.191546   0.221442 150.000000  -0.865  0.38842
centfel               1.723314   1.027115 150.000000   1.678  0.09546 .
centLRS               0.017771   0.005671 150.000000   3.134  0.00208 **
sspoly:structurenometa  -0.247813   0.302480 150.000000  -0.819  0.41393
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Final model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to degrees of
freedom [lmerMod]. Formula: longev.setup ~ ss + structure + centLRS + (1 | line)
     AIC      BIC   logLik deviance df.resid
   407.5    425.5   -197.7    395.5      144
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.4134 -0.6549 -0.0547  0.7520  2.1124
Random effects:
 Groups   Name        Variance Std.Dev.
 line     (Intercept) 0.0000   0.0000
 Residual             0.8176   0.9042
Number of obs: 150, groups:  line, 16
Fixed effects:
                 Estimate Std. Error         df t value Pr(>|t|)
(Intercept)      6.524948   0.143091 150.000000  45.600  < 2e-16 ***
sspoly           0.021188   0.149400 150.000000   0.142   0.8874
structurenometa -0.360417   0.148734 150.000000  -2.423   0.0166 *
centLRS          0.021558   0.005231 150.000000   4.121 6.21e-05 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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Chapter 6

A test of the interactive effects of sexual selection and selection associated to population spatial structure on genital evolution and sexually antagonistic coevolution

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A test of the interactive effects of sexual selection and selection associated to population spatial structure on genital evolution and sexually antagonistic coevolution

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Abstract

Genital morphology exhibits an astonishing diversification among taxa, especially in species with internal fertilization. Sexual selection has been highlighted as a key driver of such rapid and divergent evolution. Sexual conflict may lead to evolutionary 'arms races' between the sexes (sexually antagonistic coevolution), and the seed beetle *Callosobruchus maculatus* constitutes a popular model system in the study of such coevolutionary dynamics. Males possess a spiny aedeagus, which inflicts damage to the female reproductive tract during copulation. As a counteradaptation to this male-induced harm, females have evolved a thicker layer of connective tissue in their tract when the level of harm is higher, and such coevolution has been demonstrated at whithin- and between-species levels. Here we assessed sexually antagonistic coevolution concerning these genital traits in response to sexual selection and selection arising from variation in population subdivision. To this purpose we implemented a 2x2 full factorial experimental evolution approach imposing four selections regimes (combining the levels of the two formerly mentioned selection treatments) on replicated lines of *C. maculatus*. Our results show that the genital traits of both sexes responded to selection. Our results suggest that sexual conflict drives the evolution of genital spine allometry. Spine length was positively influenced by male body size, with larger males bearing longer spines regardless of the selection regime. We found that male genital spines evolved shallower static allometry (that is, they were of relatively reduced length in larger males than in smaller males) in populations with a selection history of monogamy compared to the allometry of genital spines in polygamous populations. The evolution of the amount of connective tissue lining the walls of the bursa copulatrix supported the predictions of sexual conflict in non-structured populations: females evolving under polygamy exhibited thicker walls than their monogamous counterparts. However, this evolutionary pattern was reversed in structured populations. These results provide the first empirical proof that the existence of selection associated to population spatial structure may reverse the evolutionary patterns resultant from the effects of sexual selection. Finally, the analysis of sexually antagonistic coevolution revealed positive relationships between spine length and the amount of connective tissue in the female reproductive tract in all the selection regimes but one. We are cautious, however, with interpretations from this analysis as sample size (based on selection line means) was low.

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Introduction

Genital morphology exhibits an astonishing diversification among taxa (e.g. Eberhard 2010b; Eberhard 2011 and references therein), much higher than the variation presented by many other morphological traits (Tuxen 1970; Eberhard 1985). This is also true for species with internal fertilization (Brennan 2016; Kelly and Moore 2016). Such outstanding divergence has captured the attention of the scientific community for a long time, leading to an increasing body of research aimed to assess the evolutionary mechanisms underlying such remarkable morphological variation (Arnqvist 1997, 1998; Hosken and Stockley 2004; Eberhard 2010a, b; Leonard and Córdoba-Aguilar 2010; Simmons 2014; Brennan and Prum 2015; Langerhans et al. 2016).

Genital diversity may result from pleiotropy or it may be the consequence of different selection forces, not necessarily mutually exclusive (reviewed in Eberhard 2010a; Brennan and Prum 2015). Among those forces, sexual selection has been highlighted as the main driver of such rapid and divergent evolution (Arnqvist 1998; Hosken and Stockley 2004 and references therein; Simmons 2014), because of precopulatory (e.g. Langerhans et al. 2005; Moreno-García and Cordero 2008; Grieshop and Polak 2012) and/or postcopulatory sexual selection (e.g. House and Simmons 2003; Rodriguez et al. 2004; Hotzy and Arnqvist 2009; Pitnick et al. 2010). Sexual selection may promote the diversification of the genital traits through mechanisms such as, precopulatory female choice (Grieshop and Polak 2012; Mautz et al. 2013) cryptic female choice (Eberhard 1996, 2015), sperm competition (Parker 1984; Simmons 2001) and/or sexual conflict (Parker 1979; Chapman et al. 2003; Arnqvist and Rowe 2005).

In particular, it is becoming increasingly clear that sexual conflict is an important driver of genital evolution, and by means of generating rapid evolutionary divergence in such key traits involved in reproduction, a likely engine of speciation(e.g. see Parker and Partridge 1998; Arnqvist et al. 2000; Gavrilets 2000; Gavrilets and Waxman 2002; Chapman et al. 2003; Martin and Hosken 2003b). Sexual conflict may lead to evolutionary 'arms races' between the sexes known as sexually antagonistic coevolution. Such coevolution would be generated when selection favours the expression of traits in one sex (e.g., elongation of a genital structure in males) that allow the bearers to maximize their fitness (for example providing them fertilization advantages over their rivals) at the same time that imply costs for the opposite sex (females in this example). These costs would favour the evolution of counteradaptations to prevent the harm, which in turn would favour further exaggeration of the harmful trait and son on creating a coevolutionary loop (Holland and Rice 1998; Andres and Arnqvist 2001; Arnqvist and Rowe 2002a; Evans et al. 2011; Perry and Rowe 2012; Firman et al. 2014; Perry and Rowe 2014; Wilson and Tomkins 2014).

In recent times experimental evolution has proved critical to shed light into the evolution and sexual coevolution underlying genital traits (Pitnick et al. 2001a; Pitnick et al. 2001b; Simmons et al. 2009; Cayetano et al. 2011; Simmons and Garcia-Gonzalez 2011). A useful protocol used by selection experiments focusing on the evolution of genitalia has been to remove the opportunity for sexual selection and sexual conflict by enforcing monogamy in replicated populations;

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genital traits are then assessed in individuals evolving under a polygamous mating system and compared to those from individuals evolving under monogamy. Male genital traits, including the male intromittent organ, clearly respond to the removal of sexual selection. Enforced monogamy (i.e., absence of sexual selection and sexual conflict) leads, for example, to a reduction in testes size (Pitnick et al. 2001b; Simmons and Garcia-Gonzalez 2008) or shallower static allometry regarding the length of genital spines (Cayetano et al. 2011). Recently, it has also become apparent that female genitalia also responds to sexual selection though such responses are difficult to be detected or have not been explored in detail (Brennan et al. 2007; Simmons and Garcia-Gonzalez 2011; Kotrba et al. 2014 but see Cayetano et al. 2011). In any case it is now clear that sexual selection underlies coevolutionary dynamics between male and female genital traits (Simmons and Garcia-Gonzalez 2011). In sum, experimental evolution studies have provided unambiguous evidence for the role of sexual selection on genital evolution. Comparative evidence has also supported this notion. For instance, a seminal study showed that among species, monogamous taxa tend to have relatively less complex male genital morphology than polygamous taxa (Arnqvist 1998).

Interestingly, the action of, or the opportunity for, sexual selection can be modulated by ecological factors (Evans and Garcia-Gonzalez 2016), for example through the impact of predation risk on mating systems (Heinen-Kay and Langerhans 2013; Anderson and Langerhans 2015) . Demographic features are additional paramount factors to take into account. A few studies have pointed out that reproductive isolation and speciation may evolve faster in large populations because they harbor greater levels of genetic variability and are exposed to more intense sexual selection (Gavrilets 2000; Gay et al. 2009). Another presumably important ecological and demographical aspect surrounds whether populations are panmictic or spatially structured, because, for instance, the subdivision of a population into several demes may imply limitations in regards to the number (and quality) of available mates (Yasui and Garcia-Gonzalez 2016). However, the potentially moderating effects of population spatial structure on sexual selection and sexual conflict dynamics are mostly unknown both from a theoretical and empirical perspective. In this study we aim to fill this gap. We assess the existence of sexually antagonistic coevolution in genital traits of the bean beetle *Callosobruchus maculatus* at the same time that we explore the effects of population structure selection history on coevolutionary dynamics among the sexes. This is achieved thanks to the novel application of an experimental evolution 2x2 design in which both mating system and population subdivision are manipulated.

Our model system is a suitable system for our aims because sexually antagonistic coevolution has been reported in the species due to several reasons. Males exhibit a spiny aedeagus (the male intromittent organ in insects) that damages the female reproductive tract during copulation (Crudgington and Siva-Jothy 2000), and females have evolved traits to diminish the damage inflicted by males (Edvardsson and Tregenza 2005; Rönn et al. 2007; but see Wilson and Tomkins 2014). A comparative analysis carried out by Rönn et al. (2007) on several species from the genus *Callosobruchus* showed an association between aedeagal spine length in males and the amount of connective tissue in the walls of the reproductive tract of females, which is subject to the damage inflicted by the male genital spines. Such

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elegant evidence for sexually antagonistic coevolution has been recently complemented by results at the within-species level (Dougherty et al. 2017). Here we take a step forward by asking whether such coevolutionary dynamics are influenced by mating system and population subdivision selection histories.

Material and Methods

Details about the experimental evolution protocol and the biology of the study system are thoroughly described in Chapter 1.

Below we describe the methods followed to study the joint evolution of a male genital trait that is responsible for male harm to females (length of genital spines), and a female trait that directly interacts with the harmful traits in males (thickness of the female genital tract). We measured these two genital traits in individuals from the replicated selection lines evolving under the four distinct selection regimes that we set up in our selection experiment. These selection regimes resulted from the combination of a mating system selection treatment (two levels: monogamy vs. polygamy) and a population spatial structure selection treatment (two levels: presence or absence of population subdivision).

Sexual coevolution was investigated after 18 generations of evolution under the different selection regimes. A minimum of seven individuals per sex and selection line were initially dissected (n = 117 males and 112 females). Experimental beetles were frozen immediately after collection and until they were dissected. We measured (i) the length (in micrometers) of the genital spines which cover the tip of the male aedeagus, and (ii) the thickness (measured as area of connective tissue; see below) of the females' reproductive tract lining. The connective tissue was measured in the walls of the bursa copulatrix, a specific region of the female reproductive tract that interacts with the male spiny intromittent organ during copulation (Crudgington and Siva-Jothy 2000; Rönn et al. 2007; Dougherty and Simmons 2017). Figure 6.1 shows details of male and female genitalia.

Male genital spines

Male beetles were dissected in a drop of glycerol on a slide. After extracting the genitalia from the abdomen, the spiny tip of the aedeagus was pulled out by applying pressure with extreme care on the phallic bulb. Then the forceps were moved towards the phallosome maintaining the pressure constant. Once the region with the aedeagal spines was fully everted the aedeagus was placed on a new slide with a drop of Dimethyl Hydantoin Formaldehyde (DMHF) (Steedman 1958), and covered with a coverslip whose edges were sealed to the slide with enamel at the end of the protocol.

A camera (Axiocam ERc5s, ZEISS, Germany) connected to a microscope AXIO Imager A1 (ZEISS, Germany) with lens EC Plan-NEOFLUAR 20x/0.5 (ZEISS, Germany) was used to take an image of each specimen (10x magnification). Using the software Zen 2 (blue edition) V. 2.0.0.0. (Carl ZEISS Microscopy GmbH, 2011, Germany), several of the longest genital spines were initially assessed with preliminary measurements and the length (from tip to base, see Fig. 6.1.d) of the three longest spines was measured and recorded. Repeatability of the

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measurements was calculated following Becker (1984) on a subset of individuals (n = 10) that were measured twice. The spine length values show a high repeatability (repeatability = 0.95; $p < 0.0001$).

Connective tissue of female reproductive tract walls

For females, the area of connective tissue in the walls of the bursa copulatrix was measured (in micrometres^2) with the software ImageJ (Rasband 1997). Females were processed in a Leica tp1020 Automatic tissue processor (large cycle: 16h). Females were transferred to a Leica EG1150 Modular Tissue Embedding Center where the samples were embedded in paraffin wax blocks (only one female per block to keep the females identified along the whole process). After that, the blocks were sectioned using a Leica RM2255 Fully Automated Rotary Microtome. In order to capture and account for variation in the studied area we obtained 9 cuts per individual (3 cuts from each of three zones of the bursa copulatrix in relation to the position of the pygidium -the last abdominal segment-: proximal, medial and distal, Fig 6.1a). The cuts were completely dried by keeping them at 37 °C over night. Then, the cuts were deparaffinized and rehydrated. Samples were stained with a Masson's Trichrome Kit for clinical diagnosis (AppliChem PanReac) which dyes the connective tissue in blue. Finally, the stained cuts were dehydrated and mounted using DPX mounting medium. Data from all the 9 estimates of the thickness of the reproductive tract were included in the analyses (see below). The repeatability of the measurements was calculated following Becker (1984) using a subset of cuts randomly selected, on per female, (n = 112), which were measured twice. The measurements were highly repeatable (repeatability > 0.99; $p < 0.0001$).

Male spine length was measured by one observer and the amount of connective tissue in the female reproductive tract was measured by a different person, to avoid any bias derived from the knowledge of previous results on the other sex. In addition, both measurements were blind to the origin (selection line and selection regime) to which the individual and specimens belonged.

Body size

Elytron length (EL) was used as a proxy of body size. Males and females were measured following the protocol described in Chapter 2 (Material and Methods section). Repeatability of the measurements was calculated following Becker (1984) on a subset of individuals (n = 50 per sex) that were measured twice. As found in other instances in this thesis the measurements were highly repeatable (repeatability > 0.98 ($p<0.0001$) for both sexes).

Statistical analysis

All the analyses were carried out using the software R 3.3.2 (R Core Team 2016). Linear Mixed Models (LMMs) were fitted to the untransformed variables using the function 'lmer' implemented within the package 'lme4' (Bates et al. 2015).

The models on male adaptations (spine length) and female counteradaptations (area of connective tissue) included the following variables as predictors: mating system selection treatment (monogamy/polygamy), population spatial structure selection treatment (metapopulation/no structure), and the interaction of these factors, as fixed factors. The models also included the replicate line (nested within each combination of mating system and population spatial structure; what we call

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selection regime, see Chapter 1), and the individual's ID as random factors (this later factor accounted for the fact that we had several measures, i.e., different spines in males, or estimates of reproductive tract thickness from different cuts in females, for each individual). As previously mentioned samples from three regions (proximal, medial and distal) of the bursa copulatrix from each female were processed. To account for variation due to the region of the female track from where the estimate was made we also included region (three levels) as a fixed factor in the models of female resistance (area of connective tissue). Furthermore, the models included the individual's body size (EL, see above) as a covariate. The covariate was mean centered to improve the interpretability of regression coefficients, as recommended by Schielzeth (2010).

Additionally, we analyzed the correlated evolution between male spine length and the amount of connective tissue in the walls of the bursa copulatrix of females. To this purpose, linear models (LM) were fitted on the untransformed mean area of connective tissue per line (calculated using the mean value per female within each line) using the function '*lm*' implemented in the R package '*stats*' (R Core Team 2016). In these models, we included selection regime as a fixed factor with four levels (NSPoly, Spoly, NSMono and SMono; see Chapter 1), and the mean spine length per selection line (calculated using the mean spine length per male within each line) as a covariate. The interaction between these two predictors was also included to inform on whether coevolutionary pattern differ depending on selection regimes as predicted (e.g., correlated evolution is in principle not expected in the absence of sexual conflict and sexual selection selection regimes). The covariate was mean centered as above. LMs were used for these models because we had in this case a single data point per selection line (i.e., there was no random factors involved). To calculate the significance of the main effects as well as their interaction, the argument test of the *drop1* function was set to F in these models. The multiple (i.e., without correcting for the number of predictors) and adjusted (i.e., adjusting for the number of terms in the model) R^2 values for the final LM model were obtained using the function '*summary*' implemented in the R package '*base*' (R Core Team 2016).

We also estimated static allometry of male genital spine length using ordinary least squares (OLS) regression of log-transformed spine length on log-transformed elytron length and comparing the slope estimate to isometry (Cayetano et al. 2011).

We were interested in the contribution of particular effects to variance in the dependent variables (i.e. hypothesis testing) rather than on finding the best model out of many competing ones. Thus, the focus of the analyses was to test the significance of effects. We followed the same protocol in all cases. First, we fitted the full model (the model with all the predictors and their interactions) and tested it against the null model (the model lacking the predictors of interest but including the random structure of the data, i.e., the random factors selection line and individual's identity) with a Likelihood Ratio Test (LRT) using the R function '*anova*' with argument test set to '*Chisq*'. It has been suggested that significance tests for individual predictors should only be considered once the full model reveals significance, unless an error-level adjustment for multiple testing is used to avoid inflation of Type-I error (Forstmeier and Schielzeth 2011). We adjusted *p* values for multiple testing using the Benjamini-Hochberg procedure (Benjamini

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and Hochberg 1995), to correct for such potential source of inflation of Type-I error.

We ran progressively simplified models by removing fixed effects (or their interactions) one-at-a-time using the '*drop1'* function (argument test set to '*Chi*') from the package '*stats*' (R Core Team 2016), and given our large sample sizes we tested the effect of removal of each term on the change in model deviance using LRT and maximum likelihood (Bolker et al. 2009). The final model included the significant effects (alpha criterion of 0.05), if any, and we also always retained in the final model the fixed factors mating system and structure plus the random factor selection line, regardless of the contribution of these factors, to account for the structure of the experimental design and the hierarchical structure of the data (i.e., for the fact that the data is grouped by the random factor within each combination of mating system and population structure selection levels). The effects of non-significant terms were assessed at the end of the process through a LRT comparing the final model with and without the term.

While significance of the fixed effects was calculated using maximum likelihood as described above, parameter estimates (coefficients, estimates) of the fixed and random effects in the final model were calculated using Restricted Maximum Likelihood (REML), as it has been suggested (Zuur et al. 2009). The random effect was tested with a likelihood ratio test (Lynch and Walsh 1998; Bolker et al. 2009), comparing the final model with the random term and using REML to the model without the random factor. The degrees of freedom of all the LRT and F-tests was always 1 because *drop1* compares two models (with and without the tested effect).

Pairwise comparisons among the levels within the explanatory fixed factors included in the models were carried out by mean of post-hoc Tukey tests using the function '*lsmeans*' implemented in the package with the same name (Lenth 2016).

The marginal (i.e., based on just the fixed effects) and conditional (i.e., including random effects) R^2 values for the final LMM model were calculated using the function '*sem.model.fits*' implemented in the package '*piecewiseSEM*' (Lefcheck 2016). We checked that the assumptions of the analysis (normality and homogeneity of residuals) were fulfilled by visually inspecting qqplots and plots of the distribution of the residuals against fitted values.

The general protocol for the detection and removal of influential observations and outliers (see Chapter 2) was applied before carrying out the analyses. For the spine length data set, data from 3 observations met the "influential outlier" criteria, but apart from that, some observations were removed a priori form the analysis because we could not collect the information regarding to some of the variables included in the model (e.g. absence of body size) (n=27), resulting in a final sample size of 105 males (315 spines). For the female connective tissue dataset, 3 observations met the "influential outlier" criteria and therefore they were excluded from the analysis, leading to a final sample size of 952 cuts. We also run confirmatory analysis including all data to assess whether the inclusion of what we called 'influential outliers' rendered qualitatively different results to those from the main analysis. Results were identical before and after the removal of influential outliers and we just show here the results of the main analysis excluding influential outliers, because the data in this analysis provide a better fit to the

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assumptions of normality and homoscedasticity from linear models. We report mean ± standard error values throughout. Sample sizes are also noted in tables referred to in the Results section. Tables are provided after the references. Parameter estimates and other details of the models run can be found in the Appendix at the end of the chapter.

Results

Male genital spine length and allometry

The analysis indicates the existence of a significant interaction between mating system and population spatial structure underlying spine length evolution (LRT=5.48, df = 1, p= 0.019, Fig. 6.2a and see table 6.1). Spine length did not differ between monogamous and polygamous selection histories for undivided populations (see Table 6.2), a result that fails to support predictions from sexual conflict. However, spine length did differ between individuals from different mating system selection treatments when population were subdivided; nonetheless, in this case monogamous individuals exhibited longer spines than males from polygamous selection lines (Fig. 6.2a and Table 6.2) indicating that the expected results of sexual conflict theory are actually reversed under selection stemming from population spatial structure. Spine length was also significantly affected by male body size (LRT=6.74, df = 1, p= 0.0095), with bigger males bearing longer spines (Fig. 6.3). Table 6.3 shows the male genital spine length means for each of the groups analyzed.

The slope estimate of male genital spine length on male body size was negatively allometric (slope < 1) in non-structured monogamous populations (NSMono) (slope ± standard error = 0.005 ± 0.41; t-ratio = -2.43, df = 16.79, p = 0.03), but did not differ significantly from isometry (slope = 1) in the populations evolving under the remaining selection regimes (see table 6.4 and Fig. 6.3).

Amount of connective tissue in the female bursa copulatrix

A highly significant interaction between the selection treatments of mating system and population spatial structure was also found for the female resistance trait (LRT = 14.39, df = 1, p = 0.0001; Fig. 6.2b): under a lack of selection associated to population spatial structure polygamous females exhibited thicker reproductive tracts than their monogamous counterparts, as predicted by sexual conflict. However, the pattern was reversed in subdivided populations, where monogamous, and not polygamous, females had their reproductive tracts more densely covered by connective tissue (Tabla 6.5 and Fig. 6.2b). The reversal in the pattern of sexual conflict in spatially structured populations is due to a decrease in the connective tissue of polygamous females in subdivided populations. In particular the difference in connective tissue between polygamous females belonging to the two spatial structure treatments is remarkable (see table 6.5, Tabla 6.6 and Fig 6.2b). The amount of connective tissue varied according to the region of the reproductive tract measured (LRT= 95.25, df = 1, p<0.0001), with a larger amount of connective tissue in distal and medial regions than in proximal region. The relationship between female reproductive tract and female body size was not statistically significant (see table 6.7), though there was a trend for larger

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females to have larger amounts of connective tissue. Finally, a large amount of variation in the trait measured was due to differences among females (see table 6.7). Table 6.5 shows the means of the amount of connective tissue in the female bursa copulatrix for each of the groups analyzed.

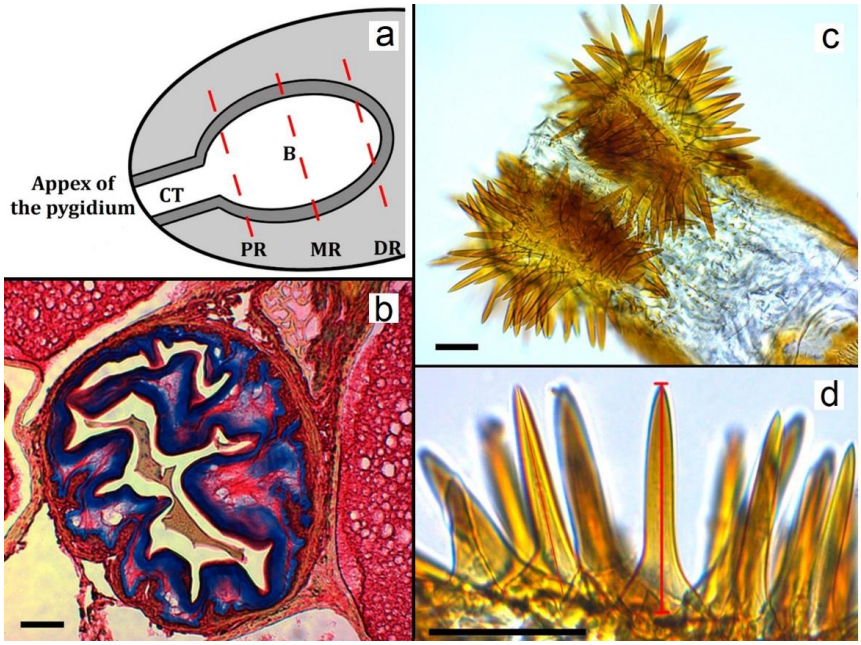

Fig. 6.1. Details of the male and female genital traits measured in *C. maculatus*: (a) A diagramatic representation of a longitudinal section of the female's abdomen: (CT) copulatory tract, (B) bursa copulatrix, (PR) proximal region, (MR) medial region and (DR) distal region of the bursa copulatrix where the cuts were carried out. Regions were named in relation to the distance with respect to the pygidium. (b) Transverse section of the female's bursa copulatrix. The connective tissue in the walls of the bursa copulatrix is stained in blue. (c) Spines covering the tip of the males' intromittent organ (aedeagus). (d) Closer detail of the male aedeagal spines. Central red line indicates the measurement of the spine length from the tip to the base. Scale bars represent 50 µm in all figures. Diagram from panel (a) drawn by Eduardo Rodriguez-Exposito. Images taken by Eduardo Rodriguez-Exposito (b) and Miguel Lozano Terol (c and d).

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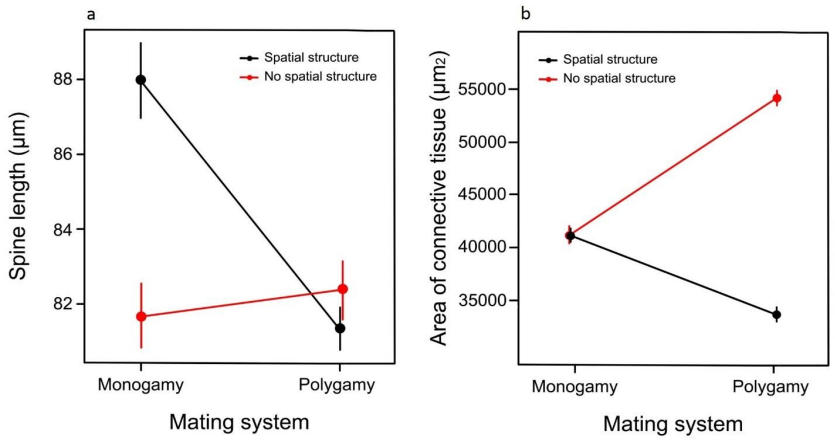

Fig. 6.2. The main and interactive effects of mating system (monogamy vs. polygamy) and spatial population structure (metapopulation structure vs. no structure) selection treatments on the length of male genital spines (a) and the area of connective tissue in the walls of the female reproductive tract (b). Circles and bars depict mean and SE calculated across the lines in each group. Data from populations with spatial structure are shown in black while data from populations without spatial structure are shown in red.

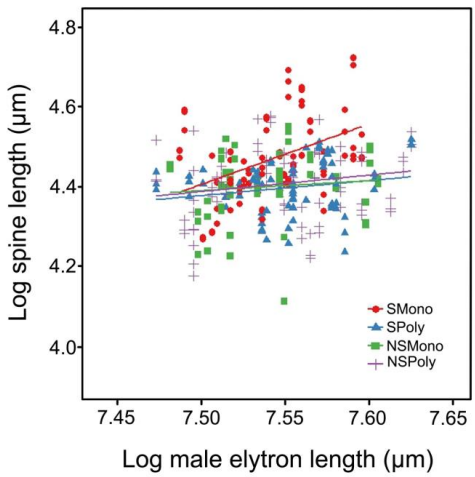

Fig 6.3. Static allometry of male genital spine length in each of our selection regimes resulting from the combination of the selection treatments mating system and population spatial structure (SMono, SPoly, NSMono, NSPoly). Solid lines represent OLS slopes.

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Correlated evolution between male and female genital traits

Selection regime had a significant effect on the amount of connective tissue ($F_{3,8}$ = 11.94, p = 0.003, Fig. 6.4). However, neither the mean male spine length, nor its interaction with the selection regime, which would be expected if there was correlated evolution in at least some selection regimes, were significant in the model (spine length: $F_{1,8}$ = 0.03, p = 0.87; interaction: $F_{3,8}$ = 1.69, p = 0.24). Nonetheless, inspection of the associations between the two variables within each selection regime (Fig. 6.4) indicate that the relationships have a positive slope (signal for correlated evolution) in all selection regimes but one: monogamous mating system in spatially structured populations.

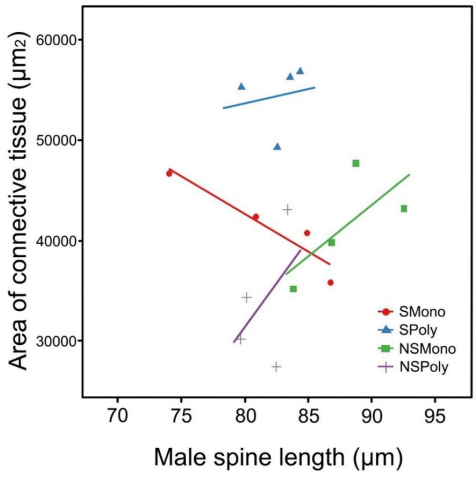

Fig. 6.4. Relationship between the amount of connective tissue in the bursa copulatrix of females and male spine length across the lines in the different selection regimes. Mean values for each selection line within each of the four selection regimes established (resulting from the combination of mating system and population spatial structure selection treatments) are shown.

Discussion

Under a scenario of strict genetic monogamy, the male and the female in a reproductive pair share their reproductive interests. However, when the possibility for polygamy exists the evolutionary interests of males and females may diverge (Parker 1979; Chapman et al. 2003; Arnqvist and Rowe 2005). In some cases males and females are immersed in a sexual 'arms race', e.g., for the control over mating decisions, which leads to coevolutionary dynamics involving the evolution of adaptations in one sex and counter-adaptations in the other (e.g. Arnqvist and Rowe 2002a; Rönn et al. 2007; Kuntner et al. 2009; Tatarnic and Cassis 2010; Simmons and Garcia-Gonzalez 2011; Perry and Rowe 2012; Yassin and Orgogozo 2013; Perry and Rowe 2014). Because the interactions between the sexes during copulation are mediated by genital traits, these traits are one of the main targets of sexually antagonistic coevolution.

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Under enforced monogamy, males do not have to compete with potential rivals for the access to females or they do not have to develop costly indicator traits to persuade females into mating. Consequently, selection under enforced monogamy applied to naturally polygamous populations should favour the reduced expression of costly traits involved in female choice, male-male competition, and/or adaptations to sexual conflict. This is indeed the rationale followed by experimental evolution studies that have demonstrated that the presence or absence of sexual selection in a population is a major factor underlying the existence of sexual conflict and underpinning the dynamics of sexually antagonistic coevolution (e.g. Holland and Rice 1999; Martin and Hosken 2003a; Firman et al. 2014).

In this study we used the seed beetle *Callosobruchus maculatus* to investigate, for the first time, the independent effects of the manipulation of sexual selection (polygamy versus monogamy) and manipulation of population spatial structure conditions (selection stemming from metapopulation structure versus no metapopulation structure), as well as their interactive effects, on the evolution and sexual coevolution of two traits directly implicated in sexual conflict in this model system: male genital spines and the amount of connective tissue in the walls of the bursa copulatrix of females (Crudgington and Siva-Jothy 2000; Crudgington 2001; Rönn et al. 2007).

The length of the genital spines that cover the surface of the tip of the aedeagus in *C. maculatus* influences male success in sperm competition (Hotzy et al. 2012). The use of phenotypic engineering in the study carried out by Hotzy et al. (2012) revealed that males with longer spines are more successful in gaining fertilizations by increasing the rate at which the ejaculate passes from the female reproductive tract to her haemolymph. Therefore, if longer spines have a positive impact on male reproductive success (Hotzy and Arnqvist 2009; Hotzy et al. 2012), and under the assumption that the expression of genital spines is costly, a reduced expression of this trait in monogamous populations, where postcopulatory sexual selection including sperm competition is absent, is expected. Such prediction has been supported in previous studies (Hotzy and Arnqvist 2009; Cayetano et al. 2011).

We found that in non-spatially structured populations genital spine length did not differ between males belonging to populations that underwent monogamous and polygamous selection. Although the pattern was for polygamous males to have slightly longer spines than monogamous males, as expected, this result fails to support the expectation from sexual conflict. These results mirror those by Cayetano et al. (2011), who did not find an effect of mating system manipulation on spine length despite a similar pattern. Interestingly, we found a significant interaction between mating system and population spatial structure underlying spine length evolution because in the presence of selection stemming from metapopulation structure there was a difference in spine length between mating system selection regimes: monogamous males exhibited longer spines than males from polygamous selection lines. These results reveal a reversal from the expectations of sexual conflict theory in spatially structured populations. Why males in monogamous spatially structured populations should evolve longer genital spines than their polygamous counterparts (see Figure 6.2) is not clear, but overall the results are in line with many other results in this thesis suggesting a reversal of sexual conflict expectations in spatially structured populations.

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Spine length was significantly influenced by male body size with larger males bearing longer spines regardless of the selection regime under which they had evolved. However, our analysis of static allometry revealed that in non-structured populations static allometry OLS slope was significantly shallower in males from monogamous selection lines than in males from polygamous selection lines, a result that matches the findings by Cayetano et al. (2011). In fact, only the OLS slope of the replicate populations evolving under the monogamous non-spatially structured selection regime (NSMono) differed from isometry, with the spines evolving at a relative lower rate as body size increases (negative allometry). These results support the notion that sexual conflict drives the evolution of genital spine allometry (Cayetano et al. 2011) and warrant further investigations into the role of sexual selection in maintaining elevated static allometry (Bonduriansky and Day 2003).

Most of the initial studies into the drivers of genital evolution focused on male genital traits exclusively. In fact, nearly double the number of studies have been carried on male, rather than female, genitalia (Ah-King et al. 2014). Some of the reasons for such bias may reside in that male genitalia was found to present much more elaborated structures (Eberhard 1985), while female genitalia was found to be less interspecifically variable than male genitalia (Eberhard 2010a, b). In addition, the female genital tract generally consists of soft tissues located inside the female body, which makes their study more difficult generally. However, female reproductive organs have been found to evolve rapidly (Puniamoorthy et al. 2010), and they present considerable variation even across closely related taxa (Pitnick et al. 1999; Anderson and Langerhans 2015). Fortunately, several studies have made a call for a greater focus on the evolution of female genitalia (Brennan et al. 2007; Kuntner et al. 2009; Evans et al. 2011; Langerhans 2011; Simmons and Garcia-Gonzalez 2011; Ah-King et al. 2014; Simmons 2014; Tanabe and Sota 2014; Anderson and Langerhans 2015). The current view is no longer that the female reproductive tract is a mere sperm-receptacle, and it is now clear that female genital traits are subject to multiple sources of selection (Eberhard 1996; Hosken and Price 2009; Simmons 2014; Brennan and Prum 2015). Furthermore, it is now clear that comparative, integrative and manipulative studies for testing the correlated evolution between male and female genitalia are required. Evidence of a positive match in the evolution of male and female genitalia has been found across many taxa, from invertebrates (Arnqvist and Rowe 2002b, a; Rönn et al. 2007; Simmons and Garcia-Gonzalez 2011; Yassin and Orgogozo 2013; Kotrba et al. 2014; Tanabe and Sota 2014) to vertebrates (Brennan et al. 2007; Brennan and Prum 2015).

Male genital spines imply damage inflicted to females during copulation (Hotzy and Arnqvist 2009), with long lasting detrimental effects to females such as a decline in their lifetime offspring production (Ronn and Hotzy 2012). Interestingly, females from the genus *Callosobruchus* have evolved "resistance" traits (Crudgington and Siva-Jothy 2000; Rönn et al. 2007; Dougherty et al. 2017 and see also Chapter 5) to minimize the extent of the male-derived injuries. In an elegant comparative study Rönn et al. (2007) unveiled sexually antagonistic coevolution between harmful male genitalia and female resistance traits in seed beetles of the genus *Callosobruchus*. These authors found that in species in which males possess longer genital spines, females are endowed with a thicker female reproductive

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tract due to the higher amount of connective tissue lining the walls of their bursa copulatrix, which is thought to ameliorate the injuries inflicted by the males' piercing aedeagus. Correlated evolution between male and female traits has been mostly detected in multi-specific studies (e.g. Arnqvist and Rowe 2002b; Koene and Schulenburg 2005; Bergsten and Miller 2007; Rönn et al. 2007; Tatarnic and Cassis 2010), while it is less frequently detected in studies at within-species level (e.g. Evans et al. 2011; Perry and Rowe 2012; Dougherty et al. 2017). This may be due to the fact that phenotypic differences among the individuals within a species are normally of a lesser magnitude than those among species. For this reason, multivariate analyses, tacking several male and female traits into account, are recommended for those studies including a single model species (Dougherty et al. 2017).

The genitalia of the females included in our study responded to selection and they did so in the way predicted by sexual conflict theory in undivided populations: polygamous females exhibited thicker reproductive tracts than monogamous females. These findings support the idea that females from polygamous populations are exposed to higher levels of male harassment and higher damage derived from copulations (perhaps due to the steeper allometry of genital spines in males, which means longer spines in larger males, which would be those presumably monopolizing the majority of matings), and that, consequently, selection favours the evolution of thicker walls in the copulatory duct to diminish the male-derived damage. Our results from selection lines without population spatial structure can be directly compared to the results in Cayetano et al. (2011) because in both studies responses to selection were assessed after 18 generations into the experimental evolution protocol and similar traits were assayed. Cayetano et al. (2011) manipulated sexual selection (imposing monogamy or not) and life-history selection (imposing early/late reproduction) in replicated populations of *C. maculatus*. While they found, as in our case, a response in the evolution of static allometry of male genitalia in agreement with the predictions from sexual selection and sexual conflict (shallower static allometry of genital spine length in monogamous populations), no detectable evolution occurred in regards to the female genital traits that they analyzed, which included the maximum thickness of the connective tissue lining of the reproductive tract. Cayetano et al. (2011) attributed these results to a delayed response in defensive traits, but in the light of our results it is possible that our measured trait (area of connective tissue in the female reproductive tract) captures better the evolution of female resistance than their measure (maximum thickness of reproductive tract walls). On the other hand, the results yielded by our analysis in subdivided populations reveal, once more, a reversal in the evolutionary pattern with respect to the results obtained for non-structured populations, and once again a reversal of the expectations based on sexual conflict theory: in spatially structured populations females that evolved under polygamy selection exhibited less connective tissue in their reproductive tract (thinner walls of the bursa copulatrix) than females evolving in the absence of sexual selection (monogamy). Again, further investigations will be required to understand the ultimate causes and mechanisms underlying these interesting results.

We found positive slopes (signal for correlated evolution) for the relationship between the female resistance and the male persistence traits in all the selection

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regimes apart from the monogamous mating system in spatially structured populations. Our results are thus suggestive of correlated evolution between the male genital spines and the amount of connective tissue lining the walls of the bursa copulatrix in female *C. maculatus.* In their work investigating the relationship between the evolution of the male genital spines and three traits related to the female resistance to male-induce harm in *C. maculatus,* Dougherty et al. (2017) also found support for sexually antagonistic coevolution at the whitin-species level. It is important to stress that in that study micro-CT X-ray scanning was used to gauge the amount of tissue in the female reproductive tract in three dimensions along the entire region contacted by the male aedeagal spines. We only used cross-sectional cuts from three regions of the bursa copulatrix. However, our measure seems to have been enough to capture variation and a signature for coevolution.

As mentioned, the analysis of sexually antagonistic coevolution, that is, the correlation between the expression of male spine length and the amount of connective tissue in the female copulatory duct showed a positive relationship for all the selection regimes except for the one imposing monogamy in spatially structured populations. Despite we did not find evidence for an interaction involving selection regime on the relationship between the male and female trait, these results suggest the existence of a signal for sexually antagonistic selection as predicted by sexual conflict theory in the presence of sexual selection (SPoly and NSPoly selection regimes). Our results that this signal is also present in monogamous non-spatially structured populations is puzzling. We are, nonetheless, cautious with interpretations from this analysis, as sample size was low due to the fact that the analysis was necessarily based on single data points per line (means calculated across the individual trait means, calculated in turn across the measures taken in each individual), so that the female trait could be related to the male trait in each line. Further analyses, for instance, carried out at other points in time (other generations of the selection experiment), or focusing on slope comparisons are warranted to shed light on the patterns found.

In summary, collectively our results are generally in agreement with the predictions from sexual conflict theory, and they are suggestive of the existence of sexually antagonistic coevolution in relation to traits determining mating interactions. Interestingly, our results are also suggestive of a reversal of sexual conflict predictions when populations are subdivided. Our results do not inform on the reasons for this reversal but they highlight the need to take into account ecological and demographical factors in the study of sexual selection and sexual conflict, and in particular they suggest that future research focusing on the role of population subdivision on sexual selection and sexual conflict dynamics will likely yield interesting insights for evolutionary knowledge. Such insights would be, in addition, paramount for the conservation biology of endangered species in spatially structured populations. Somehow, the fragmented distribution of the individuals that build up a metapopulation tend to result in a reversal of the effects related to sexual conflict dynamics in panmictic populations. These results underscore the utility of taking into account ecological and demographical features in the study of sexual selection and conflict.

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Table 6.1. Analysis of the male genital spine length. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal R^2= 0.17; conditional R^2= 0.87).

Effect	LRT	p
Mating system : structure	5.48	**0.02**
Mating system	3.74	0.053
Structure	1.68	0.20
Male elytron length	6.74	**0.01**
Line (Random)	0.08	0.77
Male Identity (Random)	268.17	**<0.0001**

Table 6.2. Tukey tests pairwise comparisons of male genital spine length in the selection regimes resulting from the interaction of mating system and population spatial structure. The degrees of freedom were calculated using Satterthwaite method.

Contrast	Estimate	SE	df	t-ratio	p
SMono- SPoly	7.03	2.32	22.11	3.04	0.03
SMono- NSMono	6.04	2.42	24.67	2.50	0.09
SMono- NSPoly	5.84	2.30	21.73	2.53	0.08
SPoly - NSMono	-0.99	2.46	25.52	-0.40	0.98
SPoly - NSPoly	-1.19	2.33	22.16	-0.51	0.96
NSMono- NSPoly	-0.20	2.44	25.16	-0.08	0.99

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Table 6.3. Means ± 1 SE and sample size (within brackets) of male aedeagal spine length (in micrometers) for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). Sample sizes indicate the number of individuals measured per group. A total of 315 spines were measured (3 spines per individual; see Methods).

Trait	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Spine Lenght (µm)	87.97 ± 1.02 (29)	81.33 ± 0.58 (27)	81.69 ± 0.87 (21)	82.37 ± 0.80 (28)	85.33 ± 0.74 (50)	81.86 ± 0.50 (55)	84.77 ± 0.65 (56)	82.08 ± 0.59 (49)

Table 6.4. Analysis of allometry regarding spine length for each selection regime resulting from the interaction between mating system and population spatial structure.

Selection regime	Estimate	SE	df	t-ratio	p
NSPoly	0.42	0.39	23.52	-1.49	0.15
NSMono	0.005	0.41	19.79	-2.43	0.03
SPoly	0.37	0.36	25.19	-1.75	0.09
SMono	1.52	0.59	25.55	0.88	0.39

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Table 6.5. Means ± 1 SE and sample size (within brackets) of the area of connective tissue in the bursa copulatrix (in square micrometers) for each level of the selection treatments mating system (Monogamy / Polygamy) and population spatial structure (Metapopulation / No metapopulation) as well as for the selection regimes resulting from the combination of the two selection treatments (SMono, Spoly, NSMono, NSPoly). Sample sizes indicate the number of females measured per group. A total of 1008 histological cuts were measured (9 histological cuts per female, excepting a few females for which some cuts could not be measured due to faulty preparation; see Methods).

Trait	SMono	SPoly	NSMono	NSPoly	Overall Monogamy	Overall Polygamy	Overall Metapopulation	Overall No Metapopulation
Area of connective tissue (μm^2)	41400.86 ± 724.02 (28)	33718.85 ± 762.16 (28)	41173,48 ± 888.60 (28)	54294.36 ± 783.71 (28)	41290,28 ± 569.56 (56)	44157.58 ± 721.63 (56)	37632.03 ± 553.28 (56)	47886,49 ± 662.94 (56)

Table 6.6. Tukey tests pairwise comparisons of the amount of connective tissue in the walls of the female reproductive tract in the selection regimes resulting from the interaction of mating system and population spatial structure. The degrees of freedom were calculated using Satterthwaite method.

Contrast	Estimate	SE	df	t-ratio	p
SMono- SPoly	7593.33	3619.09	21.30	2.10	0.19
SMono- NSMono	481.59	3620.69	21.32	0.13	0.99
SMono- NSPoly	-13347.38	3618.29	21.28	-3.69	0.0068
SPoly - NSMono	-7111.71	3622.25	21.35	-1.96	0.23
SPoly - NSPoly	-20940.71	3619.86	21.31	-5.79	0.0001
NSMono- NSPoly	-13828.98	3621.48	21.33	-3.82	0.0050

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Table 6.7. Analysis of the amount of connective tissue in the walls of the female reproductive tract. The expression 'mating system : structure' refers to the interaction between the mating system and population spatial structure selection treatments. P values are highlighted in bold if they remained significant after applying the Benjamini-Hochberg correction (see text). Variance explained by final model: marginal $R^2 = 0.31$; conditional $R^2 = 0.68$.

Effect	LRT	p
Mating system : structure	14.39	**0.0001**
Mating system	0.78	0.38
Structure	6.93	**0.01**
Region	95.25	**<0.0001**
Female elytron length	2.09	0.15
Line (Random)	2.89	0.09
Female Identity (Random)	377.74	**<0.0001**

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Appendix Chapter 6

Model: Evolution of aedeagal spine length

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: length ~ ss + structure + ss:structure + centmel
+ (1|line) + (1 | id)

     AIC      BIC   logLik deviance df.resid
  1871.6   1901.6   -927.8   1855.6      307
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.3144 -0.4940 -0.0441  0.4369  3.3775
Random effects:
 Groups   Name        Variance Std.Dev.
 id       (Intercept) 43.331   6.5827
 line     (Intercept)  0.881   0.9386
 Residual              8.215   2.8662
Number of obs: 315, groups:  id, 105; line, 16
Fixed effects:
                       Estimate Std. Error      df t value Pr(>|t|)
(Intercept)              87.681      1.350  11.840  64.957 2.22e-16 ***
sspoly                   -7.029      1.939  12.590  -3.626  0.00323 **
structurenometa          -6.041      2.059  15.820  -2.935  0.00981 **
centmel                  26.792     10.157 104.360   2.638  0.00962 **
sspoly:structurenometa    7.228      2.834  14.190   2.551  0.02289 *
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model : Identical values than full model

Model: Evolution of the amount of connective tissue in the walls of the female reproductive tract.

Full model

```
Linear mixed model fit by maximum likelihood t-tests use Satterthwaite approximations to
degrees of freedom [lmerMod]. Formula: area ~ ss + structure + ss:structure + centfel +
slide + (1|    line) + (1|femaleid)

     AIC      BIC   logLik deviance df.resid
 20111.8  20160.4 -10045.9  20091.8      942
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.9059 -0.5576  0.0162  0.5695  6.5899
Random effects:
 Groups   Name        Variance Std.Dev.
 femaleid (Intercept) 66240280 8139
 line     (Intercept)  8407002 2899
 Residual             65090560 8068
Number of obs: 952, groups:  femaleid, 112; line, 16
Fixed effects:
                       Estimate Std. Error      df t value Pr(>|t|)
(Intercept)             38509.1     2208.3    17.0  17.438  3.2e-12 ***
sspoly                  -7312.0     3085.8    16.0  -2.370 0.030663 *
structurenometa          -694.8     3085.0    16.0  -0.225 0.824652
centfel                 15683.7    10786.1   105.0   1.454 0.148902
slide2                   2432.1      651.1  5828.0   3.735 0.000189 ***
slide3                   6371.9      640.9  5834.0   9.942  < 2e-16 ***
sspoly:structurenometa  21064.1     4364.2    16.0   4.827 0.000184 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Minimal model

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: area ~ ss + structure + ss:structure + slide + (1|line) + (1|femaleid)

     AIC      BIC   logLik deviance df.resid
 20111.9  20155.6 -10047.0  20093.9      943
Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.9026 -0.5500  0.0228  0.5745  6.6068
Random effects:
 Groups   Name        Variance Std.Dev.
 femaleid (Intercept) 67345400 8206
 line     (Intercept)  8932113 2989
 Residual             65098660 8068
Number of obs: 952, groups:  femaleid, 112; line, 16
```


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```
Fixed effects:
                        Estimate Std. Error t value Pr(>|t|)
(Intercept)              38463.0     2246.4  17.122 1.016561e-65 ***
sspoly                   -7593.3     3134.6  -2.422 1.541851e-02 **
structurenometa           -481.6     3136.5  -0.154 8.779669e-01 *
slide2                    2428.4      651.2   3.729 1.920993e-04 ***
slide3                    6368.3      641.0   9.936 2.915289e-23 ***
sspoly:structurenometa   21422.3     4435.0   4.830 1.363300e-06 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


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General discussion

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Sexual selection is a major force driving the evolution of numerous behavioural, ecological and physiological traits (Parker 1979; Eberhard 1985; Andersson 1994; Hosken and Stockley 2004; Arnqvist and Rowe 2005; Andersson and Simmons 2006; Eberhard 2010a, b; Leonard and Córdoba-Aguilar 2010; Simmons 2014). Such a pervasive force has paramount implications not only at the individual level, but also for populations (e.g. Jarzebowska and Radwan 2010; Price et al. 2010; Wade 2010; Almbro and Simmons 2014), and also for reproductive isolation and speciation (Hosken and Stockley 2004; Ritchie 2007; Eberhard 2010a, b; Maan and Seehausen 2011; Simmons 2014).

Nevertheless, there are other evolutionary forces, such as viability and fecundity selection, and multiple ecological, demographical and social factors including population size, operational sex ratios, the availability of sexual partners and the spatial distribution of the individuals, which moderate the effects of sexual selection on the individuals and populations (e.g. Parker and Simmons 1996; Gavrilets 2000; Haikola et al. 2001; Kokko and Jennions 2008; Gay et al. 2009; McDonald et al. 2013; Holman 2016; Yasui and Garcia-Gonzalez 2016).

At present it is widely accepted that the spatial distribution of the individuals that build up a population has a decisive role mediating critical features of population dynamics, as well as population viability and the population's probability of extinction (Hanski 1998; Saccheri et al. 1998; Hanski 1999; Haikola et al. 2001; Nieminen et al. 2001; Hanski and Gaggiotti 2004; Akçakaya et al. 2007; Gilpin 2013). Despite that, we know very little about the implications of population subdivision for sexual selection and sexual conflict dynamics. The information we currently have in regard to this question is very limited and it is restricted to theoretical work (e.g. Yasui and Garcia-Gonzalez 2016). This thesis aims to provide empirical data to fill this important gap in knowledge. To this purpose we have used as a model system the seed beetle *Callosobruchus maculatus* and we have run a novel experimental evolution approach in which, for the first time to the best of our knowledge, the main and interactive effects of sexual selection and population spatial structure have been explored empirically. Furthermore, understanding how these two key factors interact has paramount implications in conservation, specially for those populations in which stochastic processes may have severe consequences such as small and/or isolated populations.

In this thesis we first assessed the effects of the two formerly mentioned selection treatments (sexual selection and population spatial structure) on the evolution of body size and body mass (Chapter 2), two of the most important traits of an organism due to its general tight association with body condition, survival and reproductive success. In addition, we also explored the evolution of sexual size dimorphism (SSD). Our results suggest that selection arising from variation in population spatial structure do not to have an effect on the evolution of body size, body mass or SSD. However, our study did detect an interesting effect of the presence/absence of sexual selection, on the evolution of body size and the magnitude of SSD. Male and female body size responded differently to variations of mating system. SSD increased in those populations evolving under enforced

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monogamy, while on the contrary, it decreased in those populations evolving under polygamy. Such evolutionary patterns resultant from a sex-specific response to sexual selection may reflect on the one hand, the relevance of a large male body size to outcompete potential rivals in male-male competition and on the other hand, the differential allocation of females regarding body size when they are released from the costs derived from sexual selection and multiple mating. Finally, the results yielded by our study in relation to the variation of individual's body weight revealed that the differences we observed were mainly driven by parental and/or other environmental effects rather than by selection arising from selection history, because the observed effects disappeared after applying a common garden design prior to the moment in which the experiment was carried out.

In Chapter 3 we explored the effects of the spatial subdivision and sexual selection on the evolution of female mating rates. The origin and maintenance of polyandrous behaviour (female multiple mating) has remained a conundrum for a long time. Several hypotheses suggest that the origin and evolutionary maintenance of polyandry may respond to the benefits accrued by polyandrous females, which under some circumstances might outweigh the costs derived from multiple mating. A recent theoretical study based on computer simulations suggested that a polyandrous strategy would be favoured in subdivided populations where female multiple mating can effectively work as a risk-spreading bet-hedging strategy, protecting polyandrous females against complete reproductive failure. The frequency of unsuitable mates (e.g., infertile males) have been previously identified as a key factor determining the likelihood of bet-hedging benefits associated to polyandrous behaviour (Yasui and Garcia-Gonzalez 2016). In light of this, we measured the rates of infertile mating in our populations too. Rates of infertile matings due to either female or male infertility were extremely low regardless of the selection regime. Our results also indicated that neither the mating system, nor the population spatial structure or their interaction had a sizeable effect on female mating rates, the propensity to remate or the remating interval, probably due to the lack of differences among the selection regimes in regard to the formerly mentioned male infertility rates. However, we detected a remarkable effect of the interaction between sexual selection treatments and population spatial structure affecting female longevity. Selection arising from population subdivision reversed the evolutionary pattern consistent with the predictions of sexual conflict theory observed in non-structured populations. Such a noteworthy effect was not a mere experimental artefact, and in fact, it constituted the first of multiple findings in this thesis supporting the notion that there are paramount and unexpected implications of population subdivision on sexual selection and sexual conflict dynamics (see discussion below).

Sexual selection is a key factor conditioning the probability of population's persistence through time, due to its role for the removal of deleterious mutations and the avoidance of inbreeding depression, for example. More recently, it has been theoretically suggested that population viability is contingent on the interactive effects of mating system and the level of population spatial structuring (Yasui and Garcia-Gonzalez 2016). We explored those theoretical predictions by

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measuring female productivity and longevity as proxies of the population viability (Chapter 4). The effect of spatial population structure was apparent when the short-term productivity was analyzed. However, this effect did not translate into differences in lifetime reproductive success. Mating system, on the other hand, seemed not to have any effect on productivity. In addition, this study revealed, for a second time in this thesis, a trend for an interaction between mating system and spatial structure on female longevity, pointing out once again towards an interesting but complex combined effect of these two selection treatments upon female survival. Finally, female lifespan was positively affected by female body weight, an expected result due to the fact that adult females had to survive using the resources accrued during the larval stage since we did not provide food or water to adult beetles (nor they need it as the species is facultatively aphagous, meaning that adults do not need to feed or drink).

C. maculatus has been traditionally considered a model species for the study of sexual conflict (e.g. Crudgington and Siva-Jothy 2000; Crudgington 2001; Arnqvist and Rowe 2005; Edvardsson and Tregenza 2005; Edvardsson and Canal 2006; van Lieshout et al. 2014; Wilson and Tomkins 2014; Dougherty et al. 2017). Despite the study of sexual conflict has experienced a steep increase in the last decades (Parker 1979; Chapman and Partridge 1996; Arnqvist et al. 2000; Chapman et al. 2003; Arnqvist and Rowe 2005), several critical questions have been largely neglected. For instance, the role of population subdivision on the dynamics of sexual conflict is not known. We shed some light into this gap in knowledge in the penultimate chapter of this thesis (Chapter 5), by assessing the main and interactive effects of mating system and population spatial structure on the evolution of adaptations to sexual conflict in either sex, and by exploring the evolution of male harm and female resistance (through the effects on female productivity and lifespan). Surprisingly, our study did not detect the predicted effects of sexual selection on the majority of the traits assayed. We did however detect an effect of population subdivision on traits related to sexual conflict such as kicking duration, a female behavioural trait with a function that is not completely understood. A quite relevant finding in this chapter was the significant interaction between sexual selection and population spatial structure on female productivity and female longevity when tester females were subject to lifelong cohabitation with focal males: the results indicated, again, a reversal in the evolutionary patterns resultant (and expected) from sexual selection in large populations. This result constituted the third evidence of this thesis in regard to the power of population subdivision to moderate, and even reverse, sexual selection and conflict dynamics. This chapter also brought to light the significant effect of body size on the evolution of the majority of traits related to sexual selection and sexual conflict. Finally, it also provided support to the existence of trade-offs between different biological functions, such as somatic maintenance and reproduction, which depend to some extent on a delicate balance between the costs and benefits of sexual interactions.

Sexual selection has been found to trigger antagonistic evolutionary arms races between sexes such that the development of a certain adaptation in one sex is

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matched by a counter-adaptation in the opposite sex (e.g. Rice 1996; Holland and Rice 1999; Arnqvist and Rowe 2002; Rönn et al. 2007; Perry and Rowe 2012; Yassin and Orgogozo 2013; Perry and Rowe 2014). In fat, *C. maculatus* is a popular model system in the study of such coevolutionary dynamics (Gay et al. 2010; Cayetano et al. 2011; Dougherty et al. 2017). The last chapter of this thesis (Chapter 6) focused on the analysis of the effects of sexual selection and population spatial structure (on their own and in combination) on male and female genital traits of this species thought to be involved in sexual conflict tug of wars. Male and female genital traits responded to selection. The evolution of the aedeagal spines of males seemed to be driven by sexual conflict. We detected shallower static allometry in males from monogamous populations, matching the results found in a previous study on the same species (Cayetano et al. 2011). The analysis of the evolution of the amount of connective tissue lining the walls of the bursa copulatrix, provided the fourth evidence of how population spatial structure may reverse the evolutionary patterns resultant from the effects of sexual selection. While the pattern found in the non-structured populations was in agreement with the predictions of sexual conflict theory (thicker female reproductive tracts in polygamous populations), this pattern was reversed in structured populations. Finally, we detected a positive correlation between male and female genital traits in all but one of our selection regimes. However, due to limitations in sample size (number of populations) for that analysis, we are cautious interpreting these results.

When synthesising the results from the different chapters of this thesis, thee major topics emerge that merit closer examination and may open fertile grounds for future research:

1. **Selection arising from variation in the population spatial structure reverses in some cases the evolutionary patterns resultant from the effects of sexual selection and sexual conflict.**

This effect is arguably the most relevant conclusion yielded by the present doctoral thesis. It has been detected up to four times in different and independent datasets. Each experimental assay was carried using different individuals, at different generations, and thus the results obtained in one study are independent of the results obtained in the others. In addition, we have even confirmed in Chapter 3 that this reversal effect was also consistent when assessing the same trait across generations. In all, the results suggest that this intriguing and surprising result is not a mere experimental artifact. Our findings in this regard may be especially relevant for the biology of conservation of species exhibiting metapopulation structure. Future studies should focus on studying the reversal of the expected patterns resultant form the action of sexual selection and sexual conflict, in conjunction with already known constrains derived from the subdivision of populations (limitation of the number of mates and resources, higher risks of predation during migration among patches, etc.); all these factors may modulate the viability of populations.

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Admittedly, in some cases we have not been able to explain the reasons underlying the observed effects. Despite this, our experimental evolution studies constitute the first empirical proof, to our knowledge, of the interactive role of population spatial structure and the presence or absence of sexual selection on a series of important individual- and population-level traits. It is also the first demonstration of the reversal effects driven by population subdivision. It is beyond doubt that further research is needed to shed light on the specific mechanisms underlying such reversal, and consequently this thesis should be considered a first step towards a better understanding of the factors affecting sexual selection and sexual conflict dynamics.

2. **Sexual conflict in the seed beetle *Callosobruchus maculatus*? Maybe, but not as clear as previously thought.**

Even though our study model is considered an archetypical example of sexual conflict, the absence of differences in terms of fitness (e.g., female longevity and lifetime reproductive success), as well as in relation to other traits, between the individuals evolving under monogamy and those evolving under polygamy, seems to suggest that the conflict between the interests of males and females in regards to reproduction in this species is not as clear-cut as previously thought (and see also Edvardsson and Canal 2006).

According to the predictions of sexual conflict theory, we should have observed negative effects in terms of fitness for females mated to males from polygamous populations, where the competition for mates is higher and males generally evolve to be more competitive and more harmful for females than those which evolve under enforced monogamy, where sexual selection and conflict are largely absent (e.g. Hotzy and Arnqvist 2009; Gay et al. 2010; Cayetano et al. 2011). However, our measurements of the proxies of female fitness, namely female longevity and lifetime reproductive success, carried out in Chapter 5 failed to find support for such predictions.

Despite the large number of studies that have focused their attention on the evolution of male and female traits intimately linked to sexual conflict in this species, there is still a hot debate around the function of most of these traits including, for example, the male aedeagal spines or the pericopulatory kicking behaviour of females. In relation to the male genital spines for example, some studies suggested a potential role in relation to the anchorage of males during copulation, helping the mounting males to prevent females from terminating the copulation or to hinder take-overs from rival males (Edvardsson and Tregenza 2005; Edvardsson and Canal 2006), but more recent studies failed to support such role (Ronn and Hotzy 2012). Nonetheless, they seem to have a clear effect mediating male effectiveness in sperm competition (Hotzy and Arnqvist 2009; Hotzy et al. 2012). In relation to female kicking, it was initially suggested that it served to shorten copulation, minimizing in that sense the costs of mating for females (from the genital spines of males) (e.g. Crudgington and Siva-Jothy 2000; Edvardsson and Tregenza 2005; Edvardsson and Canal 2006), but once again,

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more recent studies have failed to support this idea (Wilson and Tomkins 2014; Dougherty and Simmons 2017).

In this species, reproductive outcomes are probably determined by a delicate and complex balance among the costs derived from copulation and the direct benefits that females may accrue through multiple mating, which may be condition-dependent. While it seems to be clear that the genital spines from male *C. maculatus* damage the female reproductive tract during copulation (Crudgington and Siva-Jothy 2000), the negative effects of male-female interactions might not be so detrimental as previously thought. The results of the elegant study carried out by Hotzy et al. (2012) using a laser to manipulate the length of male genital spines revealed that males with longer spines are more successful in gaining fertilizations due to an increase in the rate at which seminal fluid passes into the female hemolymph thought the wounds they inflict in the female tract during copulation.

However, it is possible that females benefit from mating with more attractive or manipulative males (Cordero and Eberhard 2003; Head et al. 2005; Rundle et al. 2007; Garcia-Gonzalez and Simmons 2010; Zajitschek et al. 2018).

Finally, under certain conditions, such as starvation, the direct benefits obtained from the ejaculate (nutrients and water) may induce females to remate (Edvardsson 2007; Ursprung et al. 2009) and they may even imply an increase of the female lifespan (Fox 1993). Thus, as it is possible to see, the picture is complex and there are several factors to take into account when trying to decipher whether mating and female multiple mating is costly or beneficial for females of this species.

3. Support for the existence of life-history trade-offs.

A quick review of the results of the different chapters in which female longevity was measured under different conditions (baseline longevity measured without copulation and oviposition, longevity measured after copulation without possibility for oviposition, and longevity measured after copulation in combination with oviposition), indicates the different impacts that copulation itself and oviposition have on female longevity, and expose as well an existing trade-off between different biological functions such as reproduction and somatic maintenance.

The baseline longevity of the individuals from our selection lines ranged between 16-19 days for males and 22-26 for females, approximately (Chapter 5). Mating itself, in absence of possibilities for oviposition, seemed not to have severe costs in terms of longevity, even though females in Chapter 3 were given an opportunity for remating once daily until they died. However, in those assays in which females were allowed to lay eggs after copulation, their longevity fell to approximately a third of the baseline values (Chapters 4 and 5), highlighting the remarkable cost that oviposition implies for females. The lifelong cohabitation with males and the

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exposure to their sexual harassment impose extra cost for females, which once more are reflected in a detrimental effect on their longevity (Chapter 5).

Interestingly, the analysis of female fitness carried out in Chapter 5, taking into account not only their longevity but also their productivity after punctual and continuous exposure to male sexual harassment and copulations, showed a reversal in the relationship between these two variables. The alteration of this evolutionary pattern may be probably based on differences in the benefits (e.g. hydration or nutrients) and costs (physical damage, probability of infections, etc) existing for females when they are punctually or continuously exposed to male sexual activity. Consequently, the females evolving under these two experimental conditions diverge in their allocation of the available resources between reproduction and somatic maintenance/survival.

This doctoral thesis has contributed to the understanding of ecological and evolutionary factors driving sexual selection and sexual conflict dynamics. The results stemming from our experimental evolution study have answered some questions, and at the same time they have opened a new set of interesting and promising avenues for future research.

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Conclusions

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Conclusions

1. The combination of experimental evolution techniques with a suitable model system, the seed beetle *Callosobruchus maculatus*, has proved to be an excellent approach to shed light into the main and interactive effects of sexual selection and population spatial structure on a series of individual-level and population-level traits connected to sexual selection and sexual conflict.

2. While selection arising from variation in population spatial structure seems not to have a significant effect on the evolution of the individuals' body size, this phenotypic trait responds to the presence or absence of sexual selection. Importantly, a sex-specific response regarding the evolution of body size was detected, leading to a variation in the magnitude of sexual size dimorphism among our selection regimes: sexual size dimorphism increased in populations that evolved under enforced monogamy, compared to their polygamous counterparts.

3. Neither mating system, nor population spatial structure or their interaction, have a significant effect on female mating rates, the propensity to remate or the remating interval under the conditions in our selection experiment.

4. Mating system, population spatial structure or their interaction do not affect significantly population viability, at least under the conditions established in our selection experiment.

5. Patterns observed regarding female longevity are in concordance with the predictions of sexual conflict theory, but interestingly, this pattern is reversed under selection associated to metapopulation structure, evidencing thus far unappreciated far-reaching consequences of population structuring on this key life-history trait. Further analyses are required to unveil the specific causes and mechanisms underlying such reversal.

6. We assessed the main and interactive effects of population subdivision and mating system selection on the evolution of sexual conflict adaptations, including the evolution of male harm and female resistance. Our results in this regard suggest that sexual conflict in this species is not as clear-cut as previously thought.

7. We exposed a trade-off between female productivity and female longevity but the direction of the relationship changed depending on the levels of sexual interactions (punctual exposure versus lifelong exposure to males). This indicates that trade-offs between life-history traits in sexual conflict systems depends on a complex and delicate balance between the benefits and costs of sexual interactions.

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8. We explored the effects of sexual selection and population spatial structure on sexually antagonistic coevolution in genital traits. Genital traits responded to selection in both sexes and population spatial structure implied a reversal in the patterns expected under sexual conflict for the female genital trait (amount of connective tissue in the copulatory tract). Moreover, our results were suggestive of sexually antagonistic coevolution.

9. A general conclusion in this thesis, which is drawn from results gathered in different and independent experiments, assays and datasets, is that selection associated to population spatial structure reverses the expected effects of sexual selection and sexual conflict in panmictic populations. In the light of the importance of such results and their implications (e.g., for conservation biology), further analyses are warranted to unveil the specific causes and mechanisms underlying such reversal.

10. Our results have shed light on the ecological and evolutionary factors fueling, and moderating, adaptations (and counteradaptations) to sexual selection and sexual conflict. At the same time, our investigations have opened a new set of interesting questions for future research.

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