

# Metabolic adaptations for isopod specialization in three species of *Dysdera* spiders from the Canary Islands

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**Abstract.** The spider genus *Dysdera* is considered to comprise specialist isopod feeders, although the degree of specialization varies between species, depending on morphological (shape of chelicerae), behavioural (attack tactics) and metabolic (food quality of prey) adaptations. *Dysdera* has radiated extensively in the Canary Islands (currently 47 endemic species are described) and codistributed species have different cheliceral shapes and body sizes indicating different feeding niches. In the present study, we investigate the existence of metabolic adaptations to feeding on isopods by three endemic species (*Dysdera insulana* Simon, *Dysdera macra* Simon and *Dysdera verneauli* Simon) from Tenerife. We hypothesize that there is enhanced extraction efficiency of fundamental macronutrients from isopods compared with control prey in species with special morphological and behavioural adaptations for this prey type. We measure quantitatively spider growth, dry mass consumption, lipid and nitrogen consumption, and calculate growth efficiency and efficiency of utilization of dry mass, lipid and nitrogen. The results show that all three species are able to utilize both prey types, indicating that none of them are strict isopod specialist. *Dysdera insulana* shows enhanced growth efficiency and *D. macra* shows enhanced nitrogen extraction efficiency compared with *D. verneauli* when feeding on *Porcellio* rather than on *Musca*. Both traits indicate likely adaptations for the utilization of isopods. Spider species, sex and prey type all affect lipid and nitrogen extraction efficiencies, indicating that spiders do not simply extract nutrients in the proportions available. The results support the hypothesis that adaptations for enhanced digestion of focal prey evolve in species that already have adaptations for enhanced capture success.

**Key words.** Araneae, Dysderidae, metabolic adaptation, nutrition, oniscophagy, prey specialization.

## Introduction

Food specialization has evolved relatively rarely in true predators (Futuyma & Moreno, 1988; Thompson, 1994) and only in a few cases have the evolutionary processes been elucidated (Tauber & Tauber, 1987; Tauber *et al.*, 1993). Spiders conform well with this picture (Pekár & Toft, 2015). Dipterans, moths,

ants, termites, isopods and other spiders may all be focal prey for specialized spider species (Pekár & Toft, 2015). Despite their abundance in many terrestrial habitats, isopods attract very few specialized predators as a result of a suite of powerful defences (Sutton, 1972). Spiders of the genus *Dysdera* represents one such group. Given the rarity of specialization on isopods, it is of interest to study how some predators succeed in breaking these defences.

*Dysdera* species are mainly distributed over the Mediterranean, Central Europe and the Middle East (Deeleman-Reinhold & Deeleman, 1988) comprising almost 250 species (World Spider Catalog, 2016). Some species are considered to be prey specialists with isopods as their focal

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prey (Bristowe, 1941; Cooke, 1965; Řezáč & Pekár, 2007). However, no known *Dysdera* species is a strict specialist in the sense of accepting only isopods, and some species do not even prefer woodlice over other prey types (Pollard *et al.*, 1995; Řezáč *et al.*, 2008). Common to generalist spiders, they accept a wide range of prey types (Pekár & Toft, 2015). However, most truly euryphagous spiders do not readily accept isopods and perform badly on an isopod diet (Bristowe, 1941; Pekár *et al.*, 2016), indicating that special adaptations are needed to regularly include this type of prey on the menu. Some species do not even accept isopods at all (Řezáč *et al.*, 2008). Thus, adaptations to feeding on isopods may have evolved within the genus, and possibly the various stages in the evolution of specialization because isopod predators are represented among extant species. Isopods are not a common prey to generalist spiders for several reasons. They have a strong sclerotized and calcium encrusted exoskeleton with glands secreting defensive substances; together with powerful behavioural defence mechanisms (e.g. clinging to the substrate or rolling into a ball), this makes them a difficult prey to capture (Sutton, 1972). They also accumulate toxic substances and heavy metals (Hopkin & Martin, 1985). Thus, special types of adaptations are required to include isopods in the diet. Already Bristowe (1941) noted a preference of *Dysdera* for isopods, suggesting that their large chelicerae might be adaptations to specialize on isopods. Various modifications of the morphology of the chelicerae exist in the genus (Deeleman-Reinhold & Deeleman, 1988) and these modifications are interpreted as adaptations to the hunting of isopods: elongated, concave and flattened-fanged chelicerae are associated with different tactics of attack on isopods (Řezáč *et al.*, 2008). The readiness to attack isopods and the preference for them over other prey in some species (Řezáč *et al.*, 2008) indicate that behavioural adaptations are often combined with morphological adaptations. Also, metabolic adaptations have been demonstrated because some species grow and develop better on isopod-containing diets than on a reference diet of fruit flies (Řezáč & Pekár, 2007).

In the Canary Islands, the genus *Dysdera* has radiated tremendously and 47 endemic species are known (Macías-Hernández *et al.*, 2016). The cheliceral modifications described for European *Dysdera* species are also found there, together with various other morphological modifications (e.g. in shape of the cephalothorax or bulgy chelicerae). The present study aims to test whether these modifications in the Canary Island species indicate degrees of adaptation to utilization of isopod prey. We test this by means of feeding experiments with three Canarian endemic species representing different morphological modifications, in which we measure quantitatively the consumption of isopod versus control prey. The main focus is on possible metabolic adaptations. Therefore, we measure not only dry mass consumption but also lipid and protein consumption and then estimate the efficiency of utilization of dry mass, lipid and protein, aiming to determine whether adaptations to isopod prey include the enhanced extraction efficiency of these fundamental macronutrients from the prey. Our specific predictions are based on the hypothesis of Pekár & Toft (2015) suggesting that adaptations promoting prey specialization should evolve in a sequence in accordance with

the prey detection–attack–capture–consumption–digestion sequence (Endler, 1991). Thus, we expect species with prominent behavioural and morphological modifications to be more specialized metabolically than less modified species. By comparing species and sexes, we can also analyze the factors that affect the relative extraction of lipid and protein (the L:P ratio). This parameter may be a key factor in the definition of a species' nutritional niche (Behmer & Joern, 2008; Simpson & Raubenheimer, 2012). If this parameter depends only on prey type (i.e. it varies between but not within prey types), it would indicate that the spiders simply extract nutrients in the proportions available. However, if they also vary depending on the species, sex and other characteristics of the spiders, this points to the existence of more detailed adaptations for nutrient extraction.

## Materials and methods

### *The Dysdera species*

The three species were collected on Tenerife mid-October 2009 from two localities: *Dysdera verneaui* Simon 1883 and *Dysdera insulana* Simon 1883 from the laurel forest of Anaga (28.535320 N to 16.296800 E, 880 m) where they are sympatrically distributed; *Dysdera macra* Simon 1883 was collected in the North native *Pinus canariensis* forest (28.347186 N to 16.514020 E, 1425 m). There were 25 specimens (17 females and 8 males) available for *D. verneaui*, 21 specimens (11 females and 10 males) for *D. macra*, and seven specimens for *D. insulana*. *Dysdera verneaui* was chosen as the presumed 'generalist' because it shows no special morphological features in either the chelicerae or prosomal shape. Within the genus, it is a medium-sized species (live mass: males, 40–60 mg; females, 50–100 mg), with robust medium-length basal segment (BS) of the chelicerae (BS/carapace = 0.44) and short fang (F) length (F/carapace = 0.35) (N. Macías-Hernández, unpublished biometric data). *Dysdera insulana* is a large species (live mass: adults, 130–170 mg) representing the 'concave chelicerae' morphological type (Řezáč *et al.*, 2008), with the chelicerae basal segment being dorsally concave [concavity/convexity = maximal distance from fictive line between tip and base of basal segment and its dorsal surface measured in lateral view (negative for concavity, positive for convexity): –0.03 mm] and elongated fang (F/carapace = 0.40). We therefore predicted *D. insulana* to be metabolically better adapted to the utilization of isopods than *D. verneaui*. Finally, *D. macra* is a smaller species (live mass: males, 20–40 mg; females, 25–60 mg), with robust 'slightly elongated' chelicerae (BS/carapace = 0.48) and short fang length (F/carapace = 0.35). It is characterized by a peculiar morphology of the prosoma, with a 'stepped carapace' in lateral view (Arnedo & Ribera, 1999). Although there is no information available in the literature to indicate that this may also be an adaptation to isopod hunting, the possibility exists. For example, it could allow for stronger muscles of the carapace helping to bite through hard prey. We can only predict that its adaptations for predation on isopods should be at least at the same level as *D. verneaui* and possibly better.

We chose *Musca domestica* (hereafter *Musca*) as representative of 'generalist's prey' and *Porcellio scaber* (hereafter *Porcellio*) as representative of 'specialist's prey'. *Musca* is not a natural prey of *Dysdera* spp., although other Diptera species are likely to be. Most Diptera appear to be of good food quality and acceptable to other polyphagous predators, including unspecialized spiders of sufficient size to be able to catch it (Bristowe, 1941; Mayntz & Toft, 2001) and the flies were certainly an easy catch in the narrow containers used for the spiders in these experiments. Wild-type *Musca* was obtained from a laboratory culture. *Porcellio* was collected in the field at Stjær (56.12427 N to 9.95782 E), Denmark.

### Experiments

After capture, the spiders were transported to Denmark where the experiments were performed. The spiders had all starved for 4 weeks at room temperature when the experiment started. They were sexed and weighed (initial live mass). Assignment to diet treatment groups was random, except for ensuring equal numbers of females and males in each group. Spiders were held in 30-mL plastic vials with a plaster bottom approximately 2 cm in depth to maintain humidity. They were fed either *Musca* or *Porcellio*. On each feeding date (four to six times per week), the individuals were supplied with one weighed prey after the remains of the previous prey had been removed and frozen at  $-18^{\circ}\text{C}$  for subsequent lipid and nitrogen analyses. The size of *Porcellio* prey was adjusted to the size of the spider, which was not possible with *Musca*. The experiment lasted 3 weeks during November to December 2009. Prey remains were accumulated for each week and their dry mass, lipid and nitrogen content were measured. They were dried at  $60^{\circ}\text{C}$  in a vacuum oven for at least 24 h and weighed (dry mass). Subsequently, lipids were extracted by means of three baths of petroleum ether, each lasting at least 2 days. After drying in the vacuum oven for 2 days, the samples were weighed again and subjected to analysis of nitrogen content in a CN-analyzer (Na2000; Thermo Scientific, Waltham, Massachusetts). The lipid content was calculated as the difference in dry mass of the samples before and after lipid extraction. The protein content was estimated by multiplying the nitrogen content by 6.25 (AOAC, 2006).

Every week of the experimental period, specimens of the prey species were selected and their live mass, dry mass, lipid and nitrogen content were determined as described above. We attempted to achieve the full size range of the prey species represented. Relationships were established between prey live mass and dry mass, lipid and nitrogen content. All relationships were linear. If the intercepts were nonsignificant, the regressions were forced through the origin. These relationships were used to calculate the dry mass, lipid and nitrogen content of the prey offered to the spiders. By subtracting the corresponding values for the prey remains, we obtained the amounts consumed. To calculate the efficiencies of dry mass, lipid and nitrogen extracted, we corrected for unextractable nutrients in the exoskeleton: on the first day of feeding (i.e. when the spiders were assumed to have maximal hunger), we recorded whether the prey was judged to be completely eaten or not; only data from completely eaten

prey were included in the corrections. The amounts of dry mass, lipid and nitrogen consumed were assumed to be the maximally extractable from the prey. We then calculated the ratio of maximally extractable dry mass, lipid and nitrogen compared with the amounts totally offered (i.e. including the exoskeleton). The values were: (i) *Musca*: dry mass, 0.814; lipid, 0.861; nitrogen, 0.846 and (ii) *Porcellio*: dry mass, 0.488; lipid, 0.771; and nitrogen, 0.780. Subsequently, the total dry mass, lipid and nitrogen offered were multiplied by these values to give the maximally extractable amounts offered, and we calculated the efficiency of extraction as the amounts eaten divided by the extractable amounts offered. We also calculated the lipid:protein ratio (L:P ratio) of the offered and the consumed food. The L:P offered comprised the values obtained for completely eaten prey on the first day. They were very similar for the two prey types (*Musca*:  $0.189 \pm 0.006$ ,  $n = 18$ ; *Porcellio*:  $0.184 \pm 0.010$ ,  $n = 10$ ;  $t = 0.45$ ,  $P = 0.66$ ); therefore, the common value of 0.187 is used.

By definition, the quality of a prey as food for a predator reveals the degree of adaptation of that predator to the prey in question. In feeding tests, the best indicators of food quality are fitness-related life-history parameters (Toft, 2013). In the present study, we used growth efficiency (i.e. growth per unit dry mass consumed) as the main indicator of food quality because this parameter shows how well the food is transformed into spider mass. We consider dry mass and nutrient extraction efficiencies as possible explanations for differences in food quality.

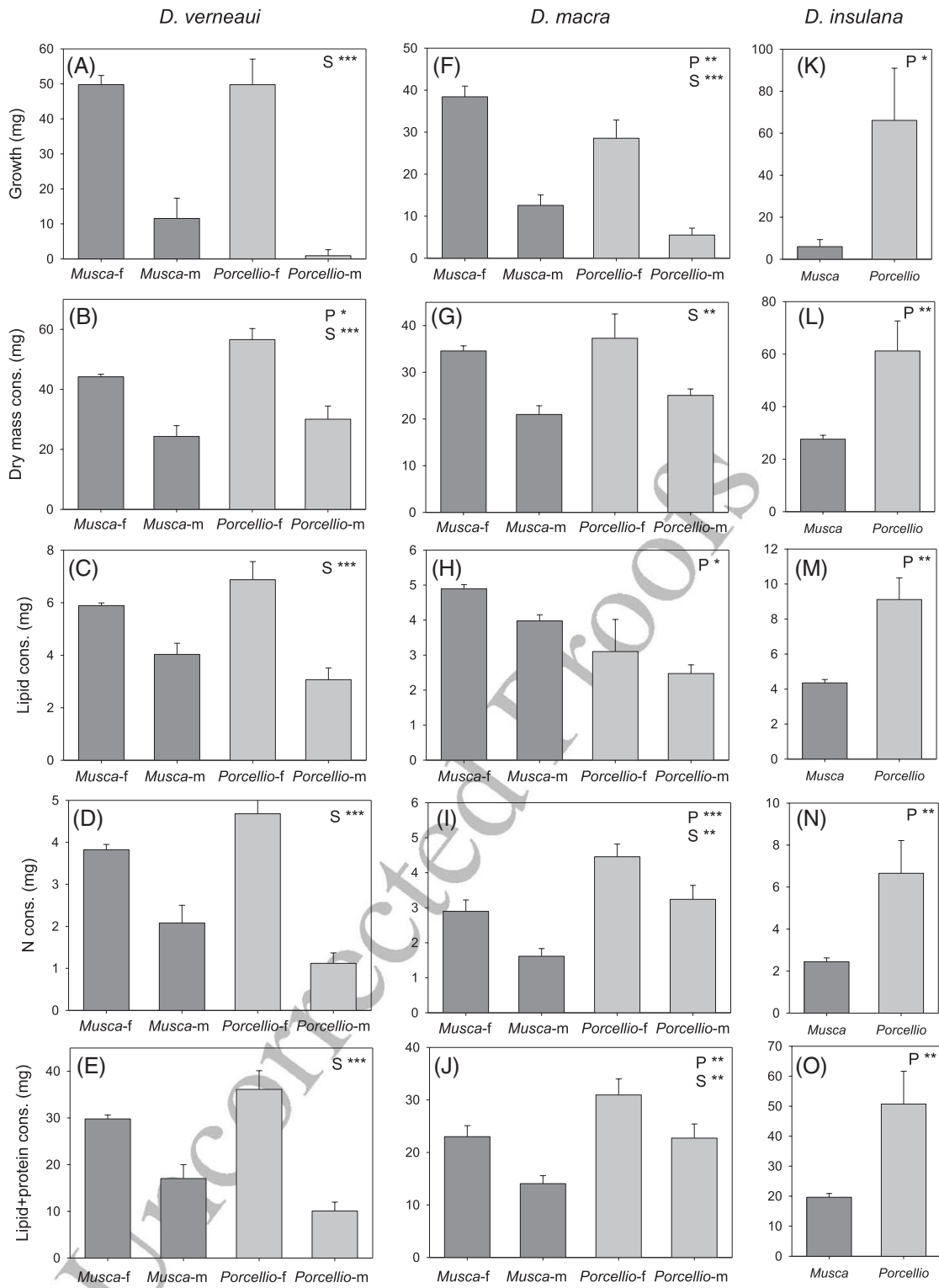
### Statistical analysis

All analyses were made in JMP, version 12 or 13 (SAS Institute Inc., Cary, North Carolina). One- or two-way analysis of covariance was used to analyze the cumulated consumption and growth data for each spider species using prey type, sex and their interaction as factors and initial live weight as covariate. Data were tested for assumptions of parametric tests; if necessary, growth and consumption data were  $\log(x + 1)$ -transformed; growth efficiency, extraction efficiencies and L:P ratio of consumed food were arcsine-square-root( $x$ )-transformed. We compared lipid and nitrogen extraction efficiencies by means of multivariate analysis of variance contrasts. Unfortunately, the number of *D. insulana* individuals available was low ( $n = 7$ ) and four of them were large juveniles. Because of the low sample sizes, we also report marginally significant  $P$ -values (Fig. 1); sex (three levels: females, males, juveniles) was initially included in the statistical analyses but was always nonsignificant and therefore is not illustrated.

## Results

### Prey effects

Growth was independent of prey type in *D. verneai* (Fig. 1a); in *D. macra*, it was highest with *Musca* as prey (Fig. 1f), whereas, for *D. insulana*, it was highest with *Porcellio* as prey (Fig. 1k). The growth efficiency (mass increase per unit dry mass



**Fig. 1.** Growth, dry mass, lipid, nitrogen and lipid + protein consumption (mean  $\pm$  SE) of three Canarian *Dysdera* species offered *Musca* and *Porcellio* (Isopoda) as prey. For *Dysdera verneaui* and *Dysdera macra*, data are presented for females (f) and males (m), separately. The statistical models included the factors prey type (P), spider sex (S), prey  $\times$  sex (P $\times$ S) and initial live weight of the spiders as covariate; only significant factors are shown: (\*):  $0.1 > P > 0.05$ ; (\*):  $0.05 > P > 0.01$ ; (\*\*):  $0.01 > P > 0.001$ ; (\*\*\*)  $P < 0.001$ .

consumed) indicated *Musca* to be superior prey for *D. verneau* and *D. macra*, and *Porcellio* to be superior prey for *D. insulana* (Fig. 2a, f, k).

Dry mass consumption of *Porcellio* was higher than of *Musca* (and significantly so for *D. verneau* and *D. insulana* (Fig. 1b, g, l). The large difference in *D. insulana* was mainly because of frequent rejection of *Musca*; even on the first day of feeding, only one of four individuals accepted the fly offered. The mass of prey remains was much larger for *Porcellio* than for *Musca* as a result of the heavy and indigestible calcareous exoskeleton of the isopod. Thus, the exoskeleton made up approximately half of the dry mass of *Porcellio* and less than 20% of *Musca* (see exact values in Materials and methods). When this was accounted for, dry mass extraction efficiency was independent of prey type for all three species (Fig. 2b, g, l).

Macronutrient consumption in *D. verneau* was independent of prey type (Fig. 1c–e), although the efficiency of lipid and nitrogen extraction was higher for *Musca* than for *Porcellio* (Fig. 2c, d). In *D. insulana*, all consumption parameters were highest for *Porcellio* (Fig. 2l–n), and all efficiencies were independent of prey type (Fig. 2m, n). In *D. macra*, lipid consumption was lower for *Porcellio* than for *Musca* (Fig. 1h), whereas nitrogen and lipid + protein consumption were highest for *Porcellio* (Fig. 1n, o). Correspondingly, lipid extraction efficiency was lower for *Porcellio* than *Musca* (Fig. 2h), whereas nitrogen extraction efficiency was higher (Fig. 2i).

The relationship between lipid and nitrogen extraction efficiencies not only varied strongly between prey types, but also was influenced by spider species and sex. The latter effects were mainly the result of a prey  $\times$  sex interaction in *D. verneau* (Table 1).

The L:P ratio of consumed food was higher than the L:P ratio of the prey offered, except for *Porcellio* consumption by *D. macra* (Fig. 2e, j, o). In *D. verneau*, the L:P ratio of consumed food was significantly influenced by sex and only marginally by prey type; in *D. macra*, it was the opposite (Table 2).

### Sex effects

In the two species with sufficient data on both sexes (*D. verneau* and *D. macra*), the increase in mass was higher in females than in males, and this was the case with both prey species (Fig. 1a, f). Accordingly, dry mass consumption and all measures of nutrient consumption showed the same pattern (Fig. 1b–e, g–j), which was also repeated for growth efficiency (Fig. 2a). In *D. verneau* but not in *D. macra*, lipid and nitrogen extraction efficiencies were higher in females than in males (Fig. 2c, d, h, i). As a result, the L:P ratio of consumed food for *D. verneau* was higher in males than in females (Fig. 2e), whereas, in *D. macra*, there was no sex difference, although there was a tendency in the same direction (Fig. 2j).

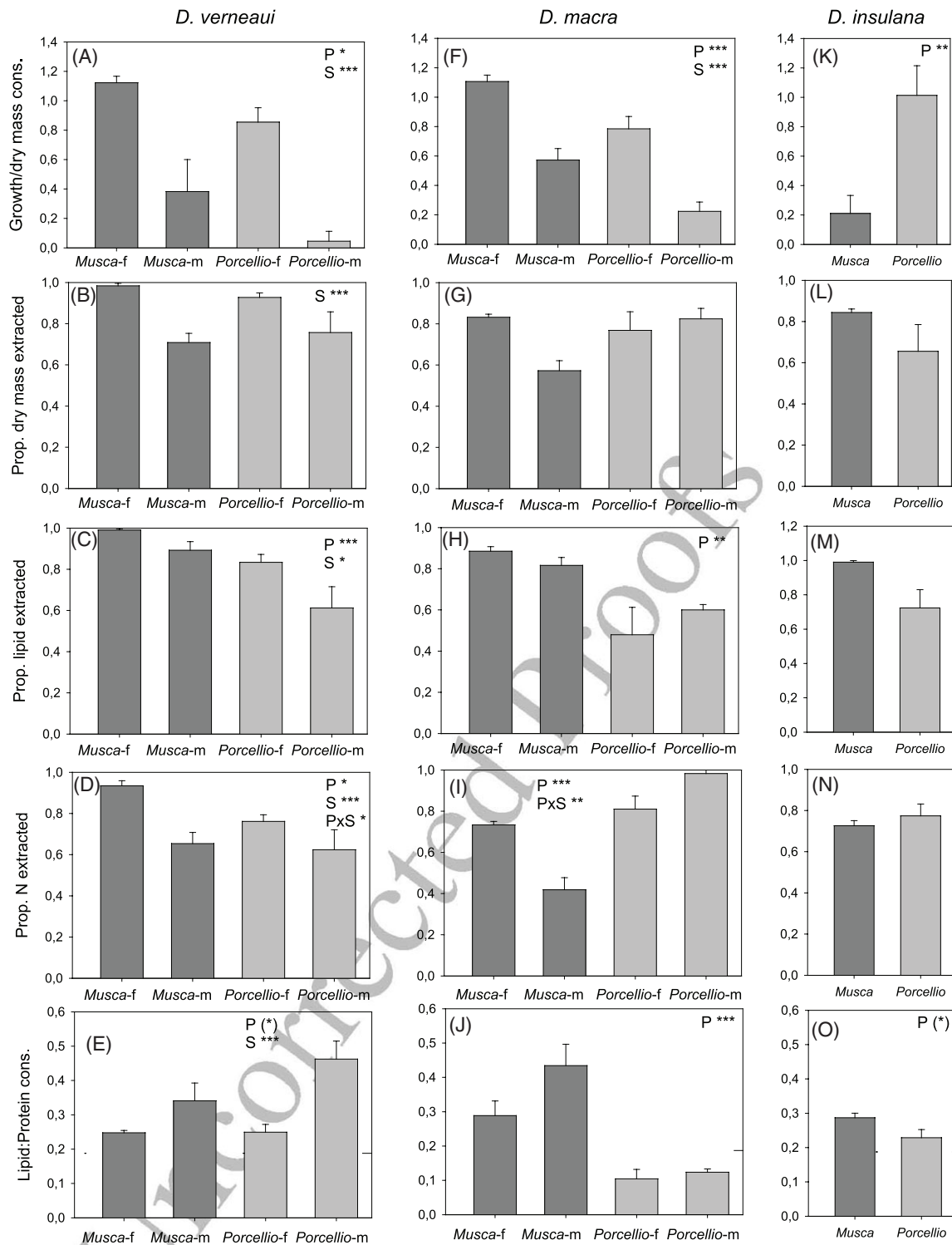
### Discussion

The results of the present study show that all three species accept and are able to utilize both house fly and isopod prey.

Thus, they have adaptations for utilizing isopods, although they are not isopod specialists in the strictest sense of complete dependence. The results also indicate that *D. insulana* is more adapted to the utilization of isopods (*Porcellio*) than *D. verneau* and *D. macra*. This is especially indicated by the higher growth efficiency for *Porcellio* than for *Musca*; in *D. verneau* and *D. macra*, it is the opposite. We found other metabolic differences between the species, although their interpretation is less obvious because they do not fall on a simple line from lower to higher degree of isopod specialization. Thus, in *D. verneau*, the L:P ratio of extracted food is higher for *Porcellio* than for *Musca*, whereas that of *D. macra* and *D. insulana* is lower in *Porcellio* than in *Musca*. This is especially a result of the higher nitrogen extraction efficiency for *Porcellio* than for *Musca* in *D. macra*. The evolution of metabolic adaptations for utilization of isopods may take different routes (i.e. the different steps need not be taken in the same order in different evolutionary lines). Overall, without implying direct evolutionary progression between these three species, our results suggest a degree of metabolic specialization for isopods in the order: *D. verneau* < *D. macra* < *D. insulana*. This order is in accordance with the predictions based on morphological modifications.

The enhanced utilization of isopod prey in *D. insulana* is expected from the cheliceral modification ('concave chelicerae' type) in this species. Concave chelicerae have been interpreted as an adaptation to the capture of isopods by allowing the spider to insert its fangs into the soft ventral side of the isopod, comprising the 'fork tactic' described in Řezáč *et al.* (2008). The species characterized for this type of chelicerae are considered as facultative isopod specialists, although they are able to consume other prey types (Řezáč *et al.*, 2008). Our results indicate that *D. insulana* is less inclined to accept flies as prey, even if hungry, and that its morphological modification to a higher extent than those in *D. verneau* and *D. macra* is accompanied by metabolic adaptations for better utilization of isopod prey. As a result of these adaptations, isopods can clearly be considered a 'focal prey' for *D. insulana* in the sense that it is a prey to which the predator has evolved specific adaptations in morphology, behaviour and physiology to enhance its utilization.

One prediction of the present study is the existence of more elaborate metabolic adaptations in *D. insulana* and possibly *D. macra* than in *D. verneau* because these species possess special morphological adaptations. The adaptation exhibited by *D. insulana* (concave chelicerae) has previously been associated with a specific attack strategy on isopods (Řezáč *et al.*, 2008). A basis of this prediction is the hypothesis proposed by Pekár & Toft (2015) that adaptations promoting prey specialization should evolve in a sequence in accordance with the prey detection–attack–capture–consumption–digestion sequence (Endler, 1991). The hypothesis predicts that behavioural adaptations (e.g. prey preference, versatility of attack) should be the first to evolve, followed by adaptations for capture (in case of *Dysdera*; e.g. cheliceral morphology), whereas metabolic adaptations (e.g. concerning nutrient extraction) should be the last to evolve. Apart from the obvious assumption that the focal prey must be nutritionally suitable in the first place to start the evolutionary process, metabolic adaptations should be



**Fig. 2.** Growth efficiency; efficiency of dry mass, lipid and nitrogen (N) extraction; and lipid:protein (L:P) ratio of consumed food (mean  $\pm$  SE) of three Canary *Dysdera* species offered *Musca* and *Porcellio* (Isopoda) as prey. For *Dysdera verneui* and *Dysdera macra*, data are presented for females (f) and males (m), separately. The statistical models included the factors prey type (P), spider sex (S), prey  $\times$  sex (P $\times$ S) and initial live weight of the spiders as covariate; only significant factors are shown: (\*):  $0.1 > P > 0.05$ ; (\*):  $0.05 > P > 0.01$ ; (\*\*):  $0.01 > P > 0.001$ ; (\*\*\*):  $P < 0.001$ . Stippled horizontal lines in (E), (J) and (O) indicate the L:P ratios of extractable food in the prey offered.

**Table 1.** Multivariate analysis of variance contrasts for difference between lipid and N extraction efficiencies, analyzed for groups of species and each species separately.

	Numerator d.f., denominator d.f.	F	P
<i>Dysdera verneai</i> + <i>Dysdera macra</i> + <i>Dysdera insulana</i>			
Whole model	8,44	14.43	<0.0001
Species	2,44	3.10	0.055
Prey	1,44	43.45	<0.0001
Sex	2,44	1.01	0.37
Species × prey	2,44	15.42	<0.0001
Initial mass	1,44	1.44	0.24
<i>Dysdera verneai</i> + <i>Dysdera macra</i>			
Whole model	8,37	15.03	<0.0001
Species	1,37	1.77	0.19
Prey	1,37	68.87	<0.0001
Sex	1,37	1.09	0.30
Species × prey	1,37	28.44	<0.0001
Species × sex	1,37	0.05	0.82
Prey × sex	1,37	9.86	0.0033
Species × prey × sex	1,37	0.31	0.58
Initial mass	1,37	2.44	0.13
<i>Dysdera verneai</i>			
Whole model	4,20	3.61	0.0226
Prey	1,20	6.08	0.0228
Sex	1,20	2.66	0.12
Prey × sex	1,20	5.88	0.0249
Initial mass	1,20	7.52	0.0125
<i>Dysdera macra</i>			
Whole model	4,16	23.00	<0.0001
Prey	1,16	85.64	<0.0001
Sex	1,16	0.01	0.94
Prey × sex	1,16	3.40	0.084
Initial mass	1,16	0.99	0.33
<i>Dysdera insulana</i>			
Whole model	2,4	5.94	0.063
Prey	1,4	10.32	0.0325
Initial mass	1,4	0.02	0.89

Significant *P*-values are indicated in bold.

prominent only in the more specialized species that more or less exclusively rely on the focal prey, whereas less specialized species must maintain their ancestral generalists' metabolic adaptations to cope with a wide diet width. Accordingly, studies of nutrient extraction from prey of the araneophagic *Portia quei*, a moderately prey-specialized spider, indicate that prey nutrient composition is more important than whether the prey belongs to the focal taxon or not (Toft *et al.*, 2010). For *Dysdera*, the hypothesis leads to the predictions that, for morphologically unmodified or little-modified species, the food quality of the 'generalist prey' (*Musca*) should be higher than or the same as that of the 'specialist prey' (=focal prey; *Porcellio* in the present study), whereas, for the more modified species, the food quality of the focal prey should be higher because of an enhanced nutrient extraction efficiency. Our results corroborate these predictions.

The exact mechanisms of the metabolic adaptations are unclear. We note, however, that the relative [*Musca:Porcellio* (M:P)] nitrogen extraction efficiency differs between the three

**Table 2.** Statistical analysis of factors affecting the lipid:protein (L:P) ratio of food consumed.

	d.f.	F	P
<i>Dysdera verneai</i>			
Full model	3,21	11.01	0.0001
Prey	1	4.03	0.058
Sex	1	27.00	<0.0001
Prey × sex	1	4.10	0.056
<i>Dysdera macra</i>			
Full model	3,17	12.07	0.0002
Prey	1	28.66	<0.0001
Sex	1	3.44	0.081
Prey × sex	1	0.62	0.44
<i>Dysdera insulana</i>			
Full model	1,5	5.36	0.068
Prey	1	5.36	0.068

L:P offered and L:P consumed were arcsine-square-root(x)-transformed. Significant *P*-values are indicated in bold.

L:P, relative extraction of lipid and protein.

*Dysdera* species: for *D. verneai*, M:P > 1; for *D. insulana*, M:P = 1; and, for *D. macra*, M:P < 1 (Fig. 2d, i, n). This is revealed without any indication of a similar pattern for lipid extraction efficiency (Fig. 2c, h, m), showing that protein and lipid extraction are to some extent independent, as is also reported by (Mayntz *et al.*, 2005). The spiders do not simply extract macronutrients in the proportion that they are available in the prey. This is also emphasized by our analyses of the factors that influence the relationship between lipid and nitrogen extraction efficiencies and the L:P ratio of the food consumed showing significant influences not only of prey type, but also of spider species, sex and their interactions (Tables 1 and 2). Given the influence of these factors, adaptations for protein and lipid extraction may also evolve independently (e.g. in relation to different prey types) to some extent.

Based on all of the above, it appears that *D. macra* is not intermediate in isopod adaptations in every aspect between *D. verneai* and *D. insulana*. It does not show enhanced growth efficiency when *Porcellio* is the prey. By contrast, in this regard it is similar to *D. verneai*. It differs from *D. verneai*, however, in demonstrating an enhanced nitrogen extraction efficiency for *Porcellio*. Further studies are needed to determine whether this can be interpreted as an isopod adaptation.

Differences in utilization efficiencies between the sexes are also prominent, particularly in *D. verneai*, although they are generally similar for the two prey types: prey and nutrient utilizations are higher for females than for males. Two prey × sex interactions are significant (Fig. 2d, i), although only one of them is representative of the opposite responses of the sexes (Fig. 2i). Growth efficiency in particular is considerably higher in females than in males (Fig. 2a, f). This means that, for every unit of food consumed, females put more into biomass than males. Males, therefore, must burn off relatively more of the food, probably via some form of activity (although this may be seriously hampered in the narrow vials used in the experiment). We do not have detailed information about the life cycle of the species but, at the time of collection (mid-October), several *D.*

1 *verneui* females had freshly laid eggs in their nests. We know  
 2 they also produce eggs during April/May. Thus, both females  
 3 and males are likely to be reproductively active (i.e. females  
 4 developing eggs, males active in mate searching) at the time  
 5 of the experiment. In accordance with expectations from the  
 6 assumption of higher activity level in males (Wilder, 2011), the  
 7 L:P ratio of consumed food is higher in males than in females,  
 8 although significantly so only in *D. verneui* (Fig. 2e, j).

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