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Prey nutrient composition has different effects on *Pardosa* wolf spiders with dissimilar life histories

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Abstract The nutritional composition of prey is known to influence predator life histories, but how the life history strategies of predators affect their susceptibility to nutrient imbalance is less investigated. We used two wolf spider species with different life histories as model predators: *Pardosa amentata*, which have a fixed annual life cycle, and *Pardosa prativaga*, which reproduce later and can extend development across 2 years. We fed juvenile spiders of the two species ad libitum diets of one of six *Drosophila melanogaster* fly types varying in lipid:protein composition during three instars, from the start of the second instar until the fifth instar moult. We then tested for interactions between predator species and prey nutrient composition on several life history parameters. *P. amentata* completed the three instars faster and grew larger carapaces and heavier body masses than *P. prativaga*, but the two species responded differently to variation in prey lipid:protein ratio. Duration of the instars increased when feeding on protein-poor prey in *P. amentata*, but was unaffected by diet in *P. prativaga*. Likewise, the effect of diet on body composition was more pronounced in *P. amentata* than in *P. prativaga*. Prey nutrient composition thus affected the two species differently. During macronutrient imbalance *P. amentata* appear to prioritize high growth rates while experiencing highly variable body compositions, whereas *P. prativaga* maintain more constant body compositions and have slower growth. These can be seen as different consequences of a fixed annual and a plastic annual–biennial life cycle.

Keywords Nutrient balance · Predator · Performance · Phenology · Lycosidae

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Introduction

Life history traits, such as rates of growth and survival, are important estimators of the fitness of an organism. They are also key components that describe the biological strategies of different species or populations of individuals (Zera and Harshman 2001). Several environmental factors may affect the life history of an organism. In spiders and other predators, it is often found that access to prey is a factor that limits growth rates and reproductive output as well as population size (Kessler 1971; Begon et al. 1990; Riechert 1992; Wise 1993). A predator with unlimited access to nutritionally balanced prey can allocate nutrients optimally to all traits and maximize fitness. However, when food is scarce or nutritionally imbalanced, the task of allocating nutritional resources to various life history traits may be

more challenging, and it is often under these situations that important aspects of life history strategies are revealed. For example, during food limitation, animals often have to trade off development time against adult size and body condition (Roff 1992; Stearns 1992; Zera and Harshman 2001), which has been documented in relation to nutrient limitation in herbivores fed nutritionally imbalanced foods (Simpson et al. 2002; Raubenheimer and Simpson 2003; Lee et al. 2004).

While the effects of prey limitation have been studied frequently, studies investigating the effects of prey nutrient composition on predators have only recently started to accumulate (Raubenheimer et al. 2007; Wilder and Rypstra 2008). In spiders, several important life history traits are known to be affected by prey nutrient composition. In the laboratory, rates of growth and survivorship were observed to be affected by the lipid and protein composition in the prey (Mayntz and Toft 2001), and in the field, the colonial web builder *Stegodyphus dumicola* increased the number of reproducing females when additional lipid-rich prey but not protein-rich prey were supplied (Salomon et al. 2008).

When challenged with inadequate diets that do not allow optimal performance in all life history traits, animals need to modify the expression of one or more life history traits compared to animals consuming more adequate diets. In arthropods, the response may involve adjustments in time spent in each instar (Raubenheimer and Simpson 1999, 2003; Mayntz et al. 2003), growth between the instars (Vollrath 1983) and/or in the number of instars used to complete development (Higgins and Rankin 1996).

We tested whether two congeneric and sympatric predators with different life histories would be differently affected by prey of variable nutrient composition. The study species were two North European wolf spiders (*Pardosa amentata* and *P. prativaga*), which co-occur in wet meadows (Nørgaard 1945; Hänggi et al. 1995) but have different cycles of development and reproduction. In Denmark, both species reproduce in the spring and early summer, but *P. amentata* are larger as adults (Roberts 1996) and reproduce earlier (May–June) and thus have a shorter time window for growth and reproduction than the smaller *P. prativaga*, which reproduce in June–September (personal observations). Furthermore, overwintering in *P. amentata* occurs predominantly as penultimate instars, whereas *P. prativaga* overwinter in several younger instars. Finally, *P. amentata* complete an annual life cycle, whereas *P. prativaga* can extend development over 2 years and thus realize a mixed annual–biennial life cycle (personal observations).

In the experiment described here, juvenile *P. amentata* and *P. prativaga* were restricted to prey of fixed nutrient composition over three instars of development. Based on the different life histories of the two species, we tested the hypothesis that the two species would show a different susceptibility to nutrient imbalance. In particular, protein limitation affects animals during growth, and fast-growing species have higher nutritional requirements than slower-growing species (McDonald et al. 2002). We predicted that *P. amentata*, with their higher growth rate and a fixed life cycle, would be more susceptible to nutritionally imbalanced prey during juvenile growth than the slower growing and developmentally more flexible *P. prativaga*.

Materials and methods

Prey types

Fruit flies (*Drosophila melanogaster*) of six different body lipid:protein compositions were produced by rearing the larvae on different media. All media were based on Carolina Instant Drosophila Medium Formula 4-24, which was (1) mixed with sucrose in a 1:4 sucrose:Carolina ratio (g:g), (2) used in its pure form, or (3) mixed with casein in a 1:9, 1:4, 2:3, or 3:2 casein:Carolina ratio, respectively. Water and a few drops of dissolved yeast were added to all media. The six fly types contained lipid:protein ratios of 0.89 ± 0.05, 0.64 ± 0.03, 0.40 ± 0.02, 0.25 ± 0.02, 0.15 ± 0.02 and 0.10 ± 0.01 [mean $\pm$ standard error (SE)], respectively. For more details on the flies and their media, the reader is referred to Jensen (2010).

General procedures

Egg sac-carrying *Pardosa amentata* and *P. prativaga* wolf spiders were caught in the low vegetation surrounding a pond at Brabrand, Denmark, and brought to the laboratory where the eggs were allowed to hatch. Two days after hatchlings had emerged, they were transferred with a paint brush to individual plastic vials (Ø = 2.0 cm, height 6 cm), each with a bottom of regularly moistened Plaster of Paris and a foam rubber stopper. To ensure that the young spiders were strong enough to catch and kill experimental fruit flies from the beginning of the experiment, we fed all hatchlings one collembolan (*Sinella curviseta*) daily from a culture reared on yeast until they moulted to the second instar. Both species were investigated simultaneously. The experiment was performed at 21–25°C.

Two days after moulting, 150 spiderlings from eight *P. amentata* egg sacs and 273 spiderlings from 12 *P. prativaga* egg sacs were weighed to the nearest microgram and distributed equally among seven treatment groups ($n = 20$–23 *P. amentata* and 39–42 *P. prativaga* per group). The spiderlings of one group were killed at the start of the experiment by freezing at −18°C, and those of the remaining six groups received one of the six different

fly types each. Fresh flies of the type decided per group were provided daily ad libitum to each spider after removing uneaten flies and checking spiders for moults and deaths. Due to a lapse in the supply of flies on the most protein-rich medium, 12 *P. prativaga* on this diet were excluded from the experiment.

Upon moulting into the fifth instar, all spiders were killed by freezing at −18°C. Carapace lengths were measured with an optical micrometer, and the spiders were dried at 60°C over 4 days and weighed. Lipids in each sample were extracted in two 24-h washes of 2 ml pure chloroform, and samples were again dried and weighed. Lipid masses were calculated by subtracting sample lean (lipid-free) dry masses from the corresponding sample dry masses. Initial carapace lengths, dry masses, lean dry masses and lipid masses of the spiders were estimated from their initial wet masses using linear regressions based on the group of spiderlings that were killed at the start of the experiment. Growth in carapace length, dry mass, lean dry mass and lipid mass from the start of the second to the start of the fifth instar were then calculated by subtracting the estimated initial values from the values measured at the end of the experiment. Relative growth rates were subsequently calculated as Δ ln carapace length or Δ ln dry mass divided by the number of days between the second and fifth moult.

Statistical analysis

Development times between the second and fifth moult (days) of surviving spiders were compared using proportional hazards tests, and these data are presented as the median ± 25th percentile. Differences in diet effects on development times between all pairs of dietary treatment groups were analysed using Bonferroni-corrected proportional hazards tests (in this case 15 $P < 0.05$). Survival of the two species across the three instars was tested with ordinal logistic regression using the number of completed instars as ordinal survival units. This test was used because the number of instars was too low to function as a continuous variable in a proportional hazards test. Growth and relative growth rates in carapace length and dry mass were tested for diet and species effects using two-way analysis of variance (ANOVA). Species-specific analyses of diet effects on growth and relative growth rates were performed using ANOVA tests, and differences between all pairs of dietary treatment groups were analysed using Tukey–Kramer tests ($P < 0.05$). Data on relative growth rates and relative lipid accumulation were arcsin transformed before analysis (Zar 1999). Differences in relative lipid accumulation between the two species within dietary treatments were analysed using *t* tests. Differences in body growth composition were analysed using multivariate ANOVA (MANOVA), with lipid accumulation and lean dry mass growth as dependent variables and spider species and prey nutrient composition as independent variables. *F* values in the MANOVA tests are exact for species effects and approximated using Wilks' λ for diet and species × diet interaction effects. All statistical analyses were performed in JMP ver. 7.0 (SAS Institute, Raleigh, NC).

Results

Pardosa amentata showed faster relative growth rates (Fig. 1d, e) due to shorter instar durations (Fig. 1a), larger carapace growth (Fig. 1b) and larger dry mass growth (Fig. 1c) than *P. prativaga* regardless of diet (Table 1). We found a significant species × diet interaction effect on the time spent in development to fifth instar (Table 1), which indicates that prey nutrient composition affected time in the instars differently in the two species (Fig. 1a). A separate analysis of the two species revealed that prey nutrient composition had a significant impact on development time in *P. amentata*, but not in *P. prativaga* (Table 2). In *P. amentata*, development was fastest on a diet of protein-rich flies and slowest on lipid-rich flies (Fig. 1a).

Survival through the three experimental instars differed significantly between the two species (Table 1), with 82% survival in *P. amentata* against 94% in *P. prativaga*. No effect of diet on survival was found (Tables 1, 2).

Increase in the carapace length (Fig. 1b) and in dry mass growth (Fig. 1c) were much higher in *P. amentata* than in *P. prativaga* (Table 1), despite both shorter carapaces (*t* test: $t_{1,58} = 20.28$, $P < 0.0001$) and smaller dry masses (*t* test: $t_{1,58} = 31.80$, $P < 0.0001$) in *P. amentata* (mean ± SE 1.03 ± 0.03 mm, 0.16 ± 0.004 mg) than in *P. prativaga* (1.11 ± 0.02 mm, 0.20 ± 0.004 mg) at the start of the experiment. Increase in carapace length was not significantly affected by diet (Table 1; Fig. 1b), but the effect of diet on dry mass growth showed a tendency for higher mass gain in spiders fed lipid-rich flies (Table 1; Fig. 1c). The rates of growth in carapace length (Table 1; Fig. 1d) and dry mass (Table 1; Fig. 1e), however, were significantly affected by diet in both species.

The composition of body growth in *P. amentata* was strongly determined by the nutrient composition of the prey, whereas this was less pronounced in *P. prativaga* (Fig. 2). Specifically, *P. prativaga* had significantly larger relative lipid growth on the three most protein-rich diets compared to *P. amentata* (*t* tests, $P < 0.001$). When analysing the effects of all diets on growth in body nutrient composition in both species simultaneously, we found a significant species × diet interaction (Table 1), indicating that the effect of prey nutrient composition on growth in body composition was more pronounced in *P. amentata* than in *P. prativaga* (Fig. 2).

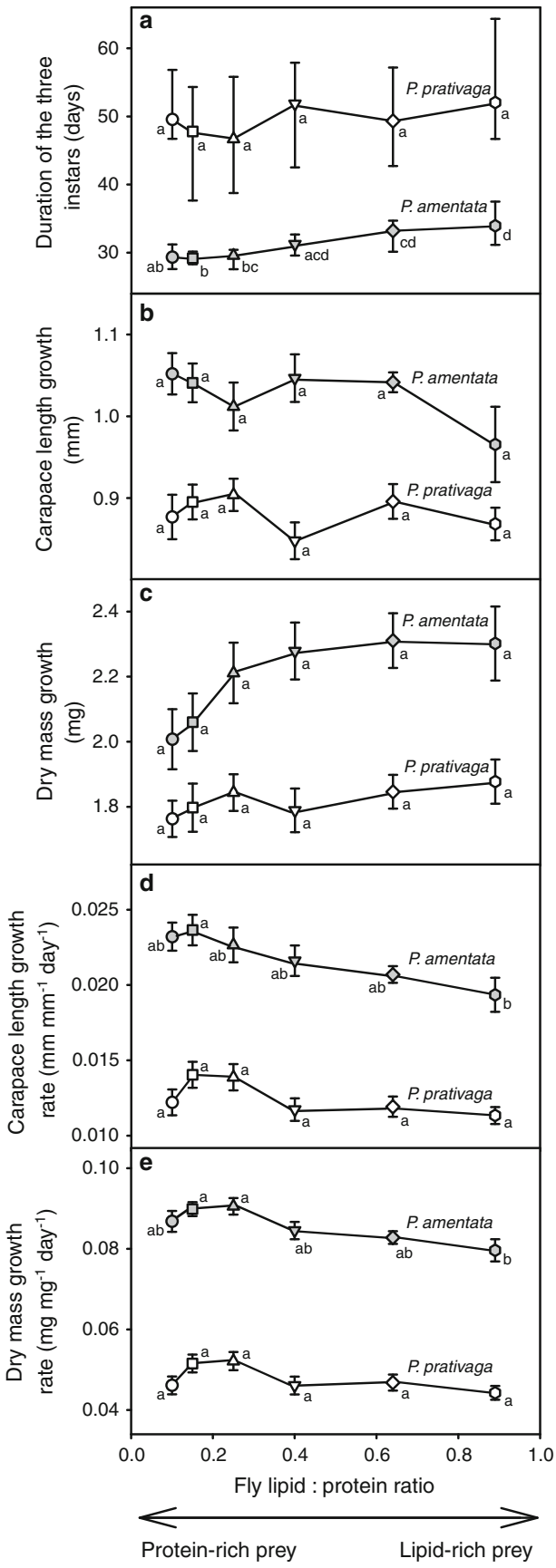

Fig. 1 The effects of prey lipid:protein composition on growth and development in *Pardosa amentata* (*gray*) and *P. prativaga* (*white*) from the second instar until the start of the fifth instar, during which the spiders were provided with monotypic diets of nutritionally manipulated *Drosophila melanogaster* under ad libitum feeding conditions. Different *letters* indicate significant differences between the groups within each species. The fly lipid:protein ratios are calculated from Jensen (2010) using a standard value of 6.25 mg protein/mg nitrogen (AOAC 2006). **a** Duration of the three instars (median ± 25th percentile). **b** Carapace length growth [mean ± standard error (SE)]. **c** Dry mass growth (mean ± SE). **d** Relative carapace length growth rate (mean ± SE), calculated as Δ ln carapace length divided by the number of days between the second and fifth moult. **e** Relative dry mass growth rate (mean ± SE), calculated as Δ ln dry mass divided by the number of days between the second and fifth moult

Discussion

Our results show that prey nutrient composition has different effects on two congeneric wolf spider species with different life history traits. Our hypothesis that a predator with fast growth and a fixed annual life cycle (*P. amentata*) would be more affected by the nutritional composition of its prey than a related species with slow growth and a flexible annual–biennial life cycle (*P. prativaga*) is thus supported. Differences in species–specific responses to prey nutrient composition were revealed by testing the interaction between spider species and prey nutrient composition on the response variable of interest. Such species-by-diet-dependent differences were found in the duration of the three experimental instars and in the composition of accumulated body nutrients.

We found that nutrient composition of the prey did not affect development time to the fifth instar in *P. prativaga*. In contrast, *P. amentata* took longer to develop on protein-poor, lipid-rich prey. One of the main differences in the life history of the two species is their growth rates. This higher sensitivity of *P. amentata* to protein deficiency may be linked to the high growth rate in this species, as protein is the main constituent required for animal tissue growth. These results are in accordance with those from another experiment, in which juvenile *P. amentata* showed susceptibility to protein deficiency in the exponential growth phase (Mayntz and Toft 2001).

Another species-dependent response to prey nutrient composition was found in the pattern of lipid and lean dry mass accumulation in the bodies of the two species during the experiment (Fig. 2). This was revealed statistically by a significant species-by-diet interaction on the accumulation of lipid and lean dry mass over the three instars (Table 1). *P. prativaga* showed smaller affects on their body compositions after feeding on prey with a high protein:non-protein energy balance. Hence, when individuals of this species were fed protein-rich flies, the lipid:lean dry mass

Table 1 Species, diet and species × diet effects on *Pardosa amentata* and *P. prativaga* fed one of six nutritionally different diets of *Drosophila melanogaster* in ad libitum amounts from the second instar until the start of the fifth instar

Statistical test	Source	Statistics		
		df		*P*
Proportional hazards on duration of the three experimental instars	Species	1	$\chi^2 = 275.83$	<0.0001
	Diet	5	$\chi^2 = 44.01$	<0.0001
	Species × diet	5	$\chi^2 = 13.85$	0.017
Ordinal logistic regression on number of instars survived	Species	1	$\chi^2 = 12.29$	0.0005
	Diet	5	$\chi^2 = 2.94$	0.71
	Species × diet	5	$\chi^2 = 1.38$	0.93
Two-way ANOVA on carapace length growth	Species	1	$F = 92.53$	<0.0001
	Diet	5	$F = 1.12$	0.35
	Species × diet	5	$F = 1.09$	0.37
Two-way ANOVA on dry mass growth	Species	1	$F = 67.40$	<0.0001
	Diet	5	$F = 2.13$	0.062
	Species × diet	5	$F = 0.84$	0.52
Two-way ANOVA on relative carapace length growth rate	Species	1	$F = 308.82$	<0.0001
	Diet	5	$F = 4.07$	0.0014
	Species × diet	5	$F = 0.65$	0.67
Two-way ANOVA on relative dry mass growth rate	Species	1	$F = 739.80$	<0.0001
	Diet	5	$F = 4.53$	0.0005
	Species × diet	5	$F = 0.31$	0.91
MANOVA on lipid growth and lean dry mass growth	Species	2,303	$F = 109.41$	<0.0001
	Diet	10,606	$F = 34.65$	<0.0001
	Species × diet	10,606	$F = 4.75$	<0.0001

(M)ANOVA, (Multivariate) analysis of variance

Table 2 Species-specific analyses of diet effects on *Pardosa amentata* and *P. prativaga*

Statistical test	Source	Species					
		Pardosa amentata			*Pardosa prativaga*		
		df		*P*	*df*		*P*
Proportional hazards on duration of the three experimental instars	Diet	5	$\chi^2 = 33.67$	<0.0001	5	$\chi^2 = 8.36$	0.14
Ordinal logistic regression on no. of instars survived	Diet	5	$\chi^2 = 1.70$	0.89	5	$\chi^2 = 2.59$	0.76
ANOVA on carapace length growth	Diet	5	$F = 1.23$	0.30	5	$F = 0.99$	0.44
ANOVA on dry mass growth	Diet	5	$F = 1.93$	0.10	5	$F = 0.60$	0.69
ANOVA on relative carapace length growth rate	Diet	5	$F = 2.64$	0.028	5	$F = 2.33$	0.044
ANOVA on relative dry mass growth rate	Diet	5	$F = 3.43$	0.0067	5	$F = 2.45$	0.035
MANOVA on lipid growth and lean dry mass growth	Diet	10,196	$F = 19.32$	<0.0001	10,408	$F = 15.53$	<0.0001

ratios of the spider bodies were higher than expected from the nutrient compositions of the ingested flies. In order to reach this composition, these spiders had a general body lipid accumulation of at least 0.3 mg over the three instars (Fig. 2). In contrast, the composition of body growth in *P. amentata* largely resembled the composition of the flies they had consumed (Fig. 2).

In order to accumulate a higher ratio of lipids in their bodies than the ratio in the flies ingested, *P. prativaga* feeding on protein-rich flies must have had different pre- or post-ingestive responses to their prey than *P. amentata* feeding on the same fly types. Pre-ingestive regulation may have occurred through a selective extraction of lipids from the prey (Mayntz et al. 2005), while post-ingestive regulation may have involved an efficient retention of lipids in combination with a high use of amino acids in metabolism (i.e., lipid sparing). In addition, excess protein may have been converted into lipids through deamination and

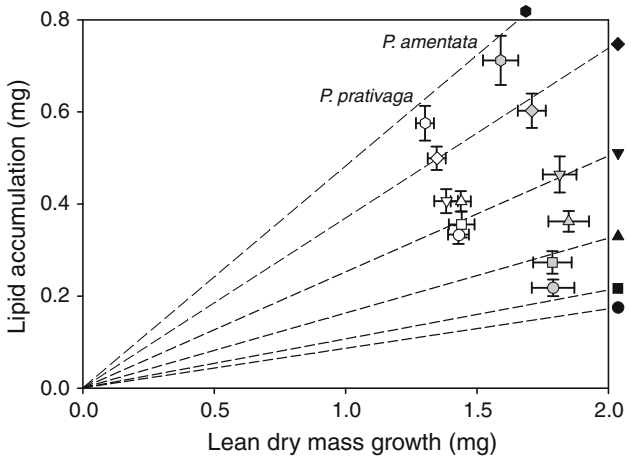

Fig. 2 Lipid accumulation and lean dry mass growth (mean ± SE) from the second instar until the start of the fifth instar in *P. amentata* (*gray*) and *P. prativaga* (*white*). The spiders were provided ad libitum diets consisting of one of six *D. melanogaster* fly types varying in lipid:protein ratio. The lipid:lean dry mass ratio of the six fly types are represented by the slopes of the *broken lines*. Each fly type is marked with a *black symbol*, and the dietary spider groups are marked with the symbol of the *fly type* with which they were provided during the experiment. The data on fly lipid:lean dry mass ratios are calculated from Jensen (2010)

lipogenesis (Stryer 1999). It is plausible to assume that the higher growth rates in *P. amentata*, in comparison to *P. prativaga*, are coupled to lower rates of lipogenesis when feeding on protein-rich prey. With these higher growth rates, *P. amentata* must have a higher need for amino acids than *P. prativaga* and may therefore have less surplus protein for lipogenesis. In addition, the higher growth rate may involve a higher net energy expenditure compared to the slower growing *P. prativaga*. Under such conditions, *P. amentata* may have to metabolize excessive amino acids to sustain energetic needs rather than directing excessive amino acids to the lipogenesis cycle.

The different degrees of fat deposition between the two spider species may also reflect differences in their feeding biology. In a study comparing specialized and generalized locust herbivores (Raubenheimer and Simpson 2003), the generalist *Schistocerca gregaria*, like *P. prativaga*, maintained fairly constant lipid stores when confined to protein-rich diets, and thus maintained a minimum lipid accumulation across a range of diets. In contrast, the grass-feeding specialist *Locusta migratoria*, like *P. amentata*, did not defend a body composition as tightly, having decreased fat stores with an increasing protein:carbohydrate ratio in the diet. These results suggest that *P. amentata* may select a more nutritionally specialized (protein-rich) diet in nature than *P. prativaga*, which would support the higher need for protein during rapid growth in *P. amentata*. Although we do not have evidence that *P. amentata* selects a more specialized diet than *P. prativaga* in nature, the larger size of *P. amentata* allows a wider range of prey capture as larger prey can be included in the diet in addition to the smaller prey (Wilson 1975; Murakami 1983). A larger size also permits exploration of a wider area, increasing encounter frequency with different prey types and thus a wider nutritional heterogeneity of the prey. Our own observations of the two species in nature and their habitat ranges (Hänggi et al. 1995) indicate that *P. amentata* may be less dependent on high humidity than *P. prativaga*, which would further allow *P. amentata* to expand its hunting area in search of prey. These differences would, in theory, provide *P. amentata* better opportunities to select a more nutritionally specialized protein-based diet in nature than *P. prativaga*.

We did not find significant effects of nutrient imbalance on the total increase in carapace length or dry mass over the three instars in any of the two species (Table 2; Fig. 1b, c). This may be caused by a high variation in size and mass growth within the instars in both species, but it may also indicate that size and mass growth between instars are tightly regulated in both species. Size growth is found to be rather tightly regulated in many arthropods (e.g., Tanaka 1981; Klingenberg and Zimmermann 1992), and critical size and mass gains are often found to be necessary for moulting (Nijhout 1981).

When the data on absolute growth and development time are combined, however, relative carapace length and dry mass growth rates in both *Pardosa* species were affected by prey nutrient composition (Table 2). Both species had higher growth rates on the more protein-rich flies (Fig. 1d, e), which indicates that a low proportion of protein limits growth rates in both species, but significance levels were much higher for *P. amentata*. It has been suggested that nitrogen (cf. amino acid) limitation is a common phenomenon in arthropod predators, especially spiders (Fagan et al. 2002; Denno and Fagan 2003; Matsumura et al. 2004). Our results support the hypothesis that predators can be nitrogen limited, but they indicate that the level of susceptibility depends on the life history strategy of the predator.

The higher growth rates in *P. amentata* appear to be associated with the cost of a higher mortality risk, which has been linked to higher developmental instability during fast growth (Arendt 1997; Higgins and Rankin 2001). A longer term experiment did show higher mortality during development in *P. amentata* fed lipid-rich compared to protein-rich *D. melanogaster* (Mayntz and Toft 2001), indicating that prey nutrient composition also affects survival in this species on a longer term.

Overall, we conclude that the different responses to imbalanced prey are most likely consequences of the different life history strategies exhibited by the two species. Whereas *P. prativaga* appear to prioritize stable lipid stores

which prolong survival if prey availability declines drastically (Jensen et al. 2010), *P. amentata* appear to prioritize fast development and high growth rate to reach early maturity and a larger size within the available season. Predators with short and strict life cycles and high growth rates may thus be more dependent on catching protein-rich prey than predators with lower growth rates and more flexible life cycles.

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References

AOAC (2006) Official methods of analysis, 18th edn. Association of Official Analytical Chemists International, Washington DC

Arendt JD (1997) Adaptive intrinsic growth rates: an integration across taxa. Q Rev Biol 72:149–177

Begon M, Harper JL, Townsend CR (1990) Ecology: individuals, populations and communities. Blackwell Scientific, Oxford

Denno RF, Fagan WF (2003) Might nitrogen limitation promote omnivory among carnivorous arthropods? Ecology 84:2522–2531

Fagan WF, Siemann E, Mitter C, Denno RF, Huberty AF, Woods HA, Elser JJ (2002) Nitrogen in insects: implications for trophic complexity and species diversification. Am Nat 160:784–802

Hänggi A, Stöckli E, Nentwig W (1995) Habitats of Central European spiders. Centre Suisse de Cartographie de la Fauna, Neuchâtel

Higgins LE, Rankin MA (1996) Different pathways in arthropod postembryonic development. Evolution 50:573–582

Higgins LE, Rankin MA (2001) Mortality risk of rapid growth in the spider *Nephila clavipes*. Funct Ecol 15:24–28

Jensen K (2010) Macro-nutrient balancing in predators: regulation of intake, utilization, and expenditure. PhD thesis. Department of Zoology, University of Oxford, Oxford

Jensen K, Mayntz D, Wang T, Simpson SJ, Overgaard J (2010) Metabolic consequences of feeding and fasting on nutritionally different diets in the wolf spider *Pardosa prativaga*. J Insect Physiol 56:1095–1100

Kessler A (1971) Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia 8:93–109

Klingenberg CP, Zimmermann M (1992) Dyar's rule and multivariate allometric growth in nine species of waterstriders (Heteroptera: Gerridae). J Zool 227:453–464

Lee KP, Simpson SJ, Raubenheimer D (2004) A comparison of nutrient regulation between solitarious and gregarious phases of the specialist caterpillar, *Spodoptera exempta* (Walker). J Insect Physiol 50:1171–1180

Matsumura M, Trafelet-Smith GM, Gratton C, Finke DL, Fagan WF, Denno RF (2004) Does intraguild predation enhance predator performance? a stoichiometric perspective. Ecology 85:2601–2615

Mayntz D, Toft S (2001) Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. Oecologia 127:207–213

Mayntz D, Toft S, Vollrath F (2003) Effects of prey quality and availability on the life history of a trap-building predator. Oikos 101:631–638

Mayntz D, Raubenheimer D, Salomon M, Toft S, Simpson SJ (2005) Nutrient-specific foraging in invertebrate predators. Science 307:111–113

McDonald P, Edwards RA, Greenhalgh JFD, Morgan CA (2002) Animal nutrition, 6th edn. Prentice Hall, Essex

Murakami Y (1983) Factors determining the prey size of the orb-web spider, *Argiope amoena* (L. Koch) (Argiopidae). Oecologia 57:72–77

Nijhout HF (1981) Physiological control of molting in insects. Am Zool 21:631–640

Nørgaard E (1945) Ecological investigations of some Danish wolf spiders. Flora Fauna 51:1–37

Raubenheimer D, Simpson SJ (1999) Integrating nutrition: a geometrical approach. Entomol Exp Appl 91:67–82

Raubenheimer D, Simpson SJ (2003) Nutrient balancing in grasshoppers: behavioural and physiological correlates of dietary breadth. J Exp Biol 206:1669–1681

Raubenheimer D, Mayntz D, Simpson SJ, Toft S (2007) Nutrient-specific compensation following diapause in a predator: implications for intraguild predation. Ecology 88:2598–2608

Riechert SE (1992) Spiders as representative 'sit-and-wait' predators. In: Crawley MJ (ed) Natural enemies—the population biology of predators, parasites and diseases. Blackwell Scientific Publications, Oxford, pp 313–328

Roberts MJ (1996) Spiders of Britain and Northern Europe. D&N Publishing, Berkshire

Roff D (1992) The evolution of life histories: theory and analysis. Chapman & Hall, New York

Salomon M, Mayntz D, Lubin Y (2008) Colony nutrition skews reproduction in a social spider. Behav Ecol 19:605–611

Simpson SJ, Raubenheimer D, Behmer ST, Whitworth A, Wright GA (2002) A comparison of nutritional regulation in solitarious- and gregarious-phase nymphs of the desert locust *Schistocerca gregaria*. J Exp Biol 205:121–129

Stearns S (1992) The evolution of life histories. Oxford University Press, Oxford

Stryer L (1999) Biochemistry, 4th edn. WH Freeman, New York

Tanaka A (1981) Regulation of body size during larval development in the German cockroach, *Blattella germanica*. J Insect Physiol 27:587–592

Vollrath F (1983) Relative and absolute growth in *Nephila clavipes*. In: Kraus O (ed) Taxonomy, biology and ecology of Araneae and Myriopoda. Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, Hamburg, pp 277–289

Wilder SM, Rypstra AL (2008) Diet quality affects mating behaviour and egg production in a wolf spider. Anim Behav 76:439–445

Wilson DS (1975) The adequacy of body size as a niche difference. Am Nat 109:769–784

Wise DH (1993) Spiders in ecological webs. Cambridge University Press, Cambridge

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice-Hall, New Jersey

Zera AJ, Harshman LG (2001) The physiology of life history trade-offs in animals. Annu Rev Ecol Syst 32:95–126