

## Foraging mode affects the evolution of egg size in generalist predators embedded in complex food webs

O. VERDENY-VILALTA\*, C. W. FOX†, D. H. WISE‡ & J. MOYA-LARAÑO\* §

\*Functional and Evolutionary Ecology, Estación Experimental de Zonas Áridas, CSIC, Almería, Spain

†Department of Entomology, University of Kentucky, Lexington, KY, USA

‡Department of Biological Sciences, and Institute for Environmental Science & Policy, University of Illinois at Chicago, Chicago, IL, USA

§Cantabrian Institute of Biodiversity, Biología de Organismos y Sistemas, Universidad de Oviedo, Oviedo, Spain

### Keywords:

egg size;  
food web;  
foraging theory;  
mobility;  
selection;  
spiders;  
trade-off.

### Abstract

Ecological networks incorporate myriad biotic interactions that determine the selection pressures experienced by the embedded populations. We argue that within food webs, the negative scaling of abundance with body mass and foraging theory predict that the selective advantages of larger egg size should be smaller for sit-and-wait than active-hunting generalist predators, leading to the evolution of a difference in egg size between them. Because body mass usually scales negatively with predator abundance and constrains predation rate, slightly increasing egg mass should simultaneously allow offspring to feed on more prey and escape from more predators. However, the benefits of larger offspring would be relatively smaller for sit-and-wait predators because (i) due to their lower mobility, encounters with other predators are less common, and (ii) they usually employ a set of alternative hunting strategies that help to subdue relatively larger prey. On the other hand, for active predators, which need to confront prey as they find them, body-size differences may be more important in subduing prey. This difference in benefits should lead to the evolution of larger egg sizes in active-hunting relative to sit-and-wait predators. This prediction was confirmed by a phylogenetically controlled analysis of 268 spider species, supporting the view that the structure of ecological networks may serve to predict relevant selective pressures acting on key life history traits.

### Introduction

Natural selection is expected generally to favour larger offspring. However, parental resources available for reproduction are frequently limited, such that allocating more resources to individual offspring (e.g. making larger eggs) comes at some cost in offspring number (Fox & Czesak, 2000). Thus, large offspring size, which positively affects offspring fitness in most organisms, trades off with offspring number, which also positively affects parental fitness (Smith & Fretwell, 1974; Fox & Czesak, 2000). A general result of theoretical models, such as

the classic Smith and Fretwell model (1974), is that when mothers control resource allocation to progeny, the offspring size favoured by selection is the size that maximizes the product of offspring fitness and maternal fecundity. Importantly, this optimum depends on the shape of the relationship between the size of an offspring and its fitness and thus varies with environmental conditions that affect this relationship.

The large number and high diversity of direct and indirect interactions that occur in food webs expose populations to complex patterns of natural selection (Gomez *et al.*, 2009; Moya-Laraño, 2012; Moya-Laraño *et al.*, 2012; Moya-Larano *et al.*, 2014). Thus, the trade-offs affecting the evolution of offspring size should be particularly complex for generalist predators that experience frequent intraguild predation, that is act simultaneously as foraging predator and potential prey. Spiders are ubiquitous generalist predators in terrestrial food

Correspondence: Oriol Verdeny-Vilalta, Estación Experimental de Zonas Áridas, EEZA-CSIC, Carretera de Sacramento s/n, 04120 La Cañada de San Urbano-Almería, Spain.  
Tel.: +34 950 281 045; fax: +34 950 277 100;  
e-mail: oriolverdeny@gmail.com

webs. Because of their high species diversity, high rates of intraguild predation and extremes of foraging mode (web builders and active hunters that never build webs) (Wise, 1993), spiders constitute an ideal model organism for testing predictions about how differences in foraging mode should affect the evolution of offspring size of organisms embedded in complex networks of species interactions. Below, we present the general arguments leading to our prediction about the evolution of offspring size of generalist predators embedded in complex food webs and why spiders are an appropriate model organism for testing our prediction.

Active foraging for resources generally exposes individuals to increased risks of predation and disease (Lima & Dill, 1990) because mobility leads to higher encounter rates among organisms. Therefore, differences in foraging mode and activity can affect the strength and diversity of predator–prey interactions (Schmitz, 2008; Moya-Laraño, 2010; Moya-Laraño *et al.*, 2013; Miller *et al.*, 2014). Variation in mobility is substantial among predators, with sit-and-wait and active hunters reflecting two extremes of a mobility continuum (e.g. Miller *et al.*, 2014). Active generalist predators are expected to encounter both prey and other predators at higher rates than are sit-and-wait predators (Huey & Pianka, 1981; Werner & Anholt, 1993; De Mas *et al.*, 2009; Moya-Laraño *et al.*, 2013). Due to higher encounter rates with prey, active predators generally have higher rates of food intake and can grow faster despite their higher metabolic rates and higher relative energy needs (Huey & Pianka, 1981; Werner & Anholt, 1993 and references therein; Miller *et al.*, 2014). However, how mobility and the associated increase in encounter rates with all of the individuals in an ecological network influence the evolution of life history traits, such as offspring size, is largely unknown.

In predator–prey interactions involving active generalist predators, body-size asymmetry largely determines who eats whom (Magalhães *et al.*, 2005; Woodward *et al.*, 2005; Wise, 2006; Brose *et al.*, 2008); thus, evolution of a larger size should make a predator more likely both to subdue prey and to escape predation. Due to energetic constraints, the abundance of animals scales negatively with body mass (Woodward *et al.*, 2005), with the result that encounters with larger animals should be less frequent because larger animals are less abundant. Therefore, for a generalist predator, slightly increasing average size reduces exposure to other generalist predators both because a greater size refuge has been achieved and because there is a lower density of predators able to kill the target individual (a size refuge *sensu* Paine, 1976). Simultaneously, larger individuals of generalist predators can subdue a larger proportion of a wide potential prey spectrum and should therefore have increased foraging success (Nentwig & Wissel, 1986; Brose *et al.*, 2008). Because mortality due

to predation is especially significant for young individuals, we expect that selection favours traits that directly increase offspring size – such as egg size – because larger offspring would be both less vulnerable as prey and more successful as predators.

We hypothesize that the benefits of being large are relatively smaller for sit-and-wait generalist predators because (i) encounters with other predators are less common due to their lower mobility, and (ii) sit-and-wait predators usually employ a set of alternative hunting strategies (e.g. traps, venoms, ambushing) that help to subdue relatively larger prey (Nentwig & Wissel, 1986). In particular, traps (e.g. webs, pitfalls) expand the rate of encounter with prey without the predator having to move at higher rates. Also, because sit-and-wait predators move less, they encounter their own predators less often, reducing the selective advantage of being larger than their predators. Active predators, on the other hand, need to move and search for prey to find them, and body-size differences should be much more important for both successfully subduing prey and avoiding other predators. Thus, the magnitude of selection favouring large body size should be greater for active-foraging predators than for sit-and-wait predators, and so the balance between selection favouring large offspring size and selection favouring high fecundity will be shifted towards a larger offspring size in active-hunting than in sit-and-wait predators. In addition, due to a trade-off between egg size and egg number, females of active-hunting species will invest in fewer eggs.

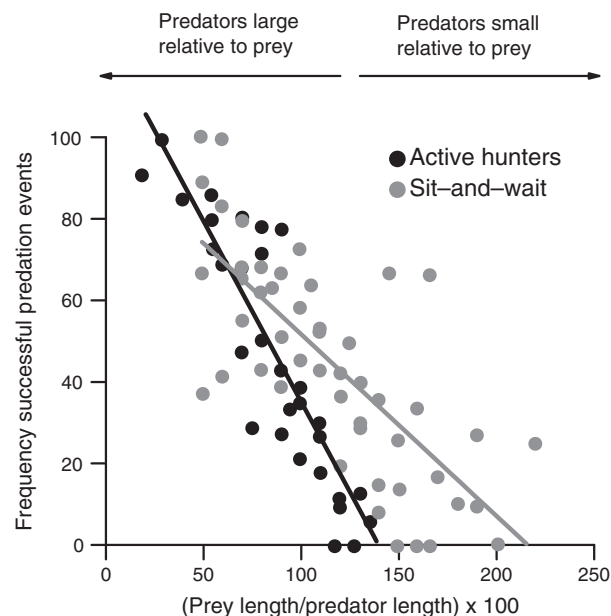
Spiders are ideal generalist predators for testing these predictions because they are speciose (Hart 2008), consume a wide variety of prey, are susceptible to predation by other spiders and can easily be divided into two categories of mobility based upon whether they use a sit-and-wait or an active-hunting mode (Schoener, 1971; Wise, 1993). Here, we use the evolutionary comparative method applied to spiders to test two predictions: *Prediction 1* – Differences in body size between prey and predator are more important in determining the outcome of a predator–prey interaction for an active generalist predator than for a sit-and-wait predator. *Prediction 2* – Selection favours large egg size more strongly for active than for sit-and-wait predators; that is, we determine whether or not the relationship between female size and egg size and the relationship between female size and clutch size have different intercepts for actively hunting and sit-and-wait predators. To test *Prediction 1*, we reanalysed the data of Nentwig & Wissel (1986) to compare predation rates between sit-and-wait and active-hunting spiders at different predator–prey size ratios. To test *Prediction 2*, we used a sample of 268 spider species (Mascord, 1970; Kaston, 1981) to compare egg size and egg number between sit-and-wait and active-hunting spiders.

## Materials and methods

### The data

Nentwig & Wissel (1986) present the percentage of interactions that led to a predation event (which is a consequence of both the willingness of the predator to attack the prey and the success of the attack) for different spider species at different predator–prey size ratios – measured as the body length of prey relative to the spider. Of the eight spider species analysed, four were sit-and-wait foragers (*Tegenaria atrica*, *Pholcus phalangioides*, *Ischnothele guyanensis* and *Xysticus cristatus*) and four were active-hunting foragers (*Pisaura mirabilis*, *Evarcha arcuata*, *Pardosa lugubris* and *Tibellus oblongus*). Prey was either crickets (*Acheta domestica*) or flies (species not specified) offered once per day. If the prey was not consumed, a smaller prey was offered the following day; if that prey was consumed, a larger prey was offered the following day. We extracted data from scans of graphs in Fig. 1 of Nentwig & Wissel (1986) using ImageJ (Schneider *et al.*, 2012).

To test *Prediction 2*, we used a data set of 268 spider species from 38 families compiled from two biogeographic regions – nearctic (Kaston, 1981) and Australasia (Mascord, 1970; Hawkeswood, 2003). From these publications, we calculated female prosoma length and width (mm), egg diameter (mm) and number of eggs



**Fig. 1** Frequency of successful predation events for different levels of the prey–predator body-size ratios in active-hunting and sit-and-wait spiders. A steeper relationship means that a unit decrease in prey–predator ratios entails higher hunting success. Based upon data from figure 1 of Nentwig & Wissel (1986).

per clutch. Prosoma width and length were obtained using a calliper to measure drawings (Kaston, 1981) or photographs of each species (Mascord, 1970; Hawkeswood, 2003) to the nearest 0.01 mm. These estimates were then rescaled relative to the average body lengths reported in the same literature (Moya-Laraño *et al.*, 2008). For some spider species ( $N = 114$ ), we lacked information on either egg size or egg number; therefore, sample sizes differed for egg size ( $N = 159$ ) and clutch size ( $N = 195$ ).

### Foraging mode and female body size

We assigned each species to either sit-and-wait or active-foraging mode based upon information by De Mas *et al.* (2009), Kaston (1981), Prenter *et al.* (1998, 1997). Although there is a continuum of foraging modes and mobilities among spiders (De Mas *et al.*, 2009), and food availability may affect mobility and exposure to predators (Huey & Pianka, 1981), sit-and-wait spiders move and change positions at lower rates than active-hunting spiders.

Because our analyses revealed differences in body shape between active-hunting and sit-and-wait spiders, we used prosoma area approximated as the product of length and width as a predictor of body size. We then rescaled prosoma area to the linear dimension by square-root transformation. Finally, to make the relationship between female size and egg parameters linear, we transformed data to their natural logarithms.

### Phylogenetically corrected statistical analysis

As species are related phylogenetically, species data points are not statistically independent and phylogenetic distances should be taken into account in the statistical analysis (Felsenstein, 1985; Paradis, 2006). We used Mesquite 2.7 (Maddison & Maddison, 2011) to assemble a phylogenetic tree from diverse literature sources to estimate the phylogenetic correlation structure as a means to correct for phylogenetic dependence (Paradis, 2006). The basic tree structure (from suborder to family level) was built using the information available in the study by Coddington (2005) and Maddison & Schulz (2007). When available, additional phylogenetic information (up to genus or species level) was also incorporated (Scharff & Coddington, 1997; Griswold *et al.*, 1998, 1999; Bosselaers & Jocque, 2000, 2002; Fang *et al.*, 2000; Hormiga, 2000; Hedin & Maddison, 2001; Levi, 2002; Agnarsson, 2003, 2004, 2006; Maddison & Hedin, 2003; Arnedo *et al.*, 2004, 2007; Benjamin, 2004; Garb *et al.*, 2004; Miller & Hormiga, 2004; Coddington, 2005; Murphy *et al.*, 2006). Other-ways, species were incorporated in the tree as soft polytomies (Purvis & Garland, 1993).

To test *Prediction 1*, we first calculated the slopes and intercepts of the linear adjustment between percentage

of prey consumed and percentage of body length of prey relative to the spider for each of the eight species of Fig. 1 in the study by Nentwig & Wissel (1986). Then, we used phylogenetic generalized least squares – which includes the phylogenetic correlation structure as the distance matrix – to compare whether the estimated slopes of the active-hunting spiders are steeper than the slopes of the sit-and-wait spiders, and whether the intercepts differed between the two foraging modes. To test *Prediction 2*, we constructed a statistical model using phylogenetic generalized least squares. First, we used the lowest AIC to determine which of the three most-common models of evolution, Brownian, Pagel or Ornstein–Uhlenbeck (Table 1, Paradis, 2006), better described the evolution of egg size and egg number. We then set the most appropriate evolutionary model as the minimum model for testing each hypothesis and proceeded to find the most parsimonious model structure by adding interactions and/or covariates, again using the lowest AIC (Table 2).

The phylogenetic tree used to test *Prediction 2* contains a large number of soft polytomies (129 nodes were unsolved across the tree). Thus, we analysed the data using the method of Martins (1996), which is most useful when the true phylogeny is not well known. We created a statistical population of 1000 random trees in which we randomly solved the uncertainty of our trees (i.e. the polytomies) and used the branch-length transformation of Grafen (1989) as a starting point before applying any branch-length transformation based upon an evolutionary model. We then estimated the same statistical parameters as in phylogenetic generalized least squares but using the simulated trees. Using joint and conditional probabilities (Martins, 1996), we obtained *P*-values for the null hypothesis that the estimated regression slopes (*b*) were not different from zero. With this procedure, one obtains a normal distribution of estimates from which the mean represents the most accurate estimate describing the relationship between the dependent variable and the predictors. We applied this method for (i) selecting the evolutionary model that best fits our data; (ii) selecting the most parsimonious statistical model relating traits to predictors; (iii) calculating estimates of slopes and the *P*-values associated with them; and (iv) plotting the

**Table 2** Interaction terms and covariates that yield the minimum statistical model for testing the predicted hypothesis.

	AIC	SE <sub>AIC</sub>
Egg size		
AP + FM + AP × FM	−154.73	0.04
AP + FM + AP × FM + BA	−165.37	0.03
AP + FM + AP × FM + BA + AP × BA*	−181.71	0.03
AP + FM + AP × FM + BA + AP × BA + FM × BA	−179.91	0.03
Fecundity		
AP + FM + AP × FM	402.35	0.04
AP + FM + BA	388.17	0.04
AP + FM + AP × FM + BA	387.97	0.04
AP + FM + AP × FM + BA + AP × BA*	380.36	0.04
AP + FM + AP × FM + BA + AP × BA + FM × BA	381.41	0.04

AP, area of the prosoma; FM, foraging mode; BA, biogeographic area.

The statistical model for testing the effects was selected by the lowest AIC. Standard error of AIC corresponds to the AIC variation due to phylogenetic uncertainty. The independent variable follows the model name.

\*Model with the lowest AIC showing the most parsimonious evolutionary model.

estimated effects and 95% confidence intervals using the procedures of Fox (2003).

We used R 3.1.0 (R Core Team, 2014) and the packages ‘ape’ and ‘nlme’ for statistical analyses.

## Results

### Prediction 1

The difference in body size between predators and their prey had a larger effect on the outcome of an interaction for active-hunting than for sit-and-wait spiders (Fig. 1). In general, active-hunting spiders needed to be larger than did sit-and-wait spiders for an interaction to lead to successful predation; sit-and-wait predators could subdue larger prey relative to their body size. Also, the slope of the relationship between successful predation and the prey/predator body-length ratio is 2× steeper for active-hunting spiders (mean slopes = −0.99 and −0.50 for active-hunting and sit-and-wait spiders, respectively;  $t_6 = 5.97$ ,  $P = 0.001$ ). Thus, a unit decrease in prey–predator body-size ratio

**Table 1** Selection of the best evolutionary model using the lowest AIC, with its standard error due to phylogenetic uncertainty.

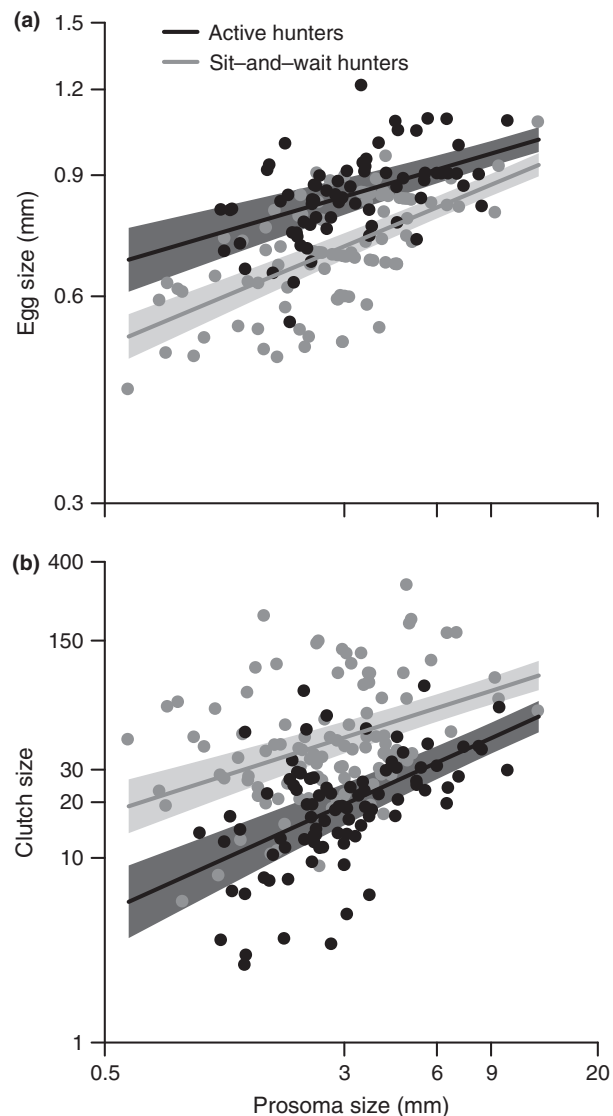
Statistical models	Evolutionary model AIC							
	None	Brownian	Pagel	Ornstein–Uhlenbeck				
Egg Size	−130.93	−56.11	0.11	−138.98	0.03	−142.28*	0.03	
Fecundity	421.37	495.51	0.08	400.91	0.01	394.68*	0.04	

\*Model with the lowest AIC showing the most parsimonious evolutionary model.

produces a greater increase in predation success for active-hunting than for sit-and-wait spiders. In addition, active-hunting spiders are better than sit-and-wait spiders at subduing and killing prey that are relatively smaller than them (mean intercepts = 132.34 and 102.95 for active-hunting and sit-and-wait spiders, respectively;  $t_6 = -2.65$ ,  $P = 0.038$ ).

### Prediction 2

Sit-and-wait spiders lay both more and smaller eggs than do active-hunting spiders of the same size (female



**Fig. 2** Effect plot of the phylogenetic generalized least squares model for the 'body size  $\times$  foraging mode' interaction in (a) egg-size model ( $n = 159$ ) and (b) clutch-size model ( $n = 195$ ). Thick lines are the partial slopes, and the shaded areas above and below the effect, the 95% confidence limits of the slopes.

size  $\times$  foraging mode interaction Fig. 2, Table 3). Although sit-and-wait spiders lay more and smaller eggs across the entire range of female sizes, egg size and egg number become more similar between the two foraging modes as female size increases (Fig. 2, Table 3). The smallest active-hunting spiders lay 1.3 $\times$  larger and 0.33 $\times$  fewer eggs than do sit-and-wait spiders, whereas the largest active-hunting spiders lay only 1.1 $\times$  larger and 0.60 $\times$  fewer eggs than do sit-and-wait spiders of comparable size.

### Discussion

Our results support the hypothesis that, for populations of generalist predators embedded in food webs consisting of both prey that need to be subdued and predators that need to be avoided, increased activity of offspring leads to the evolution of larger egg sizes. Also, likely as a direct consequence of this selection for large offspring size and the fundamental trade-off between offspring size and number, active foraging leads to the evolution of lower fecundity. Our findings strongly suggest that the quality of an environment and the selection imposed by an environment on life history traits depend on the myriad of biotic interactions that individuals experience. The study of ecological networks (Bascompte, 2009), especially from an evolutionary perspective, may help disentangle the selective gradients responsible for the evolution of life history traits.

Many taxa exhibit plastic variation in offspring size – that is females produce different-sized offspring – in response to differences in predation risk, with larger offspring favoured under higher post-hatching predation

**Table 3** Phylogenetic generalized least squares predictors and their estimated effects for the best statistical models of the hypotheses.

	Estimate	SE	<i>t</i>	<i>P</i> -value
<b>(a) Egg size (<math>n = 159</math>)</b>				
Intercept	-0.25	0.07	-3.71	0.000
Area prosoma	0.14	0.04	3.21	0.002
Foraging mode	-0.12	0.06	-1.98	0.055
Biogeographic area	-0.22	0.05	-4.10	0.000
Area prosoma $\times$ Foraging mode	0.19	0.04	4.33	0.000
Area prosoma $\times$ Biogeographic area	0.11	0.04	2.76	0.008
<b>(b) Fecundity (<math>n = 195</math>)</b>				
Intercept	2.29	0.30	7.76	0.000
Area prosoma	1.10	0.21	5.32	0.000
Foraging mode	1.09	0.23	4.75	0.000
Biogeographic area	-0.25	0.26	-0.96	0.349
Area prosoma $\times$ Foraging mode	-0.45	0.17	-2.58	0.013
Area prosoma $\times$ Biogeographic area	0.65	0.20	3.18	0.002

rates. For example, predator cues induce females to produce larger eggs or cause a delay in hatching date [e.g. salamanders (Sih & Moore, 1993; Moore *et al.*, 1996), fish (Jones *et al.*, 2003), anurans (Laurila *et al.*, 2002) and crustaceans (Blaustein, 1997)]. These adaptive responses result in offspring hatching at a larger size or in a more developed stage, changes that increase their survival when predation is size specific (Petranka *et al.*, 1987). Other studies have shown that when predator threat is absent, as is the case for salmon in hatcheries, selection favours higher fecundity and smaller egg size (Heath *et al.*, 2003). This plasticity and strong selection favouring large offspring size strongly suggest that an evolutionary response favouring large offspring size may have occurred across taxa, as demonstrated in this study. Thus, understanding how ecological interactions affect individual fitness can help us predict the evolution of important life history traits such as egg size and number.

Our comparative analysis contrasting spider taxa of distinct foraging modes (extremes in a mobility continuum) demonstrates that active-hunting spiders need to be larger (relative to prey size) to subdue prey than do sit-and-wait predators. We also found that, after taking into account female size, active-hunting spiders lay larger but fewer eggs compared to sit-and-wait spiders. These results are consistent with the prediction that active-hunting spiders will have higher fitness when offspring are born slightly larger. In addition, as expected due to the egg size/egg number trade-off, active-hunting females, which invest in larger offspring, necessarily lay relatively fewer eggs.

Investing in relatively large hatchlings may be adaptive in active-hunting spiders because of (i) the enhanced hunting ability and lower susceptibility to attacks by other predators, and (ii) the negative size–abundance relationship in food webs means that densities of potential predators will be lower and densities of available prey higher. Reaching a size refuge may be less important for sit-and-wait spiders because their reduced mobility is usually associated with lower encounter rates with predators. From our foraging analysis, we suggest that, in addition to a greater predation success, larger offspring of active-hunting spiders will be less frequently preyed upon when encountering intraguild predators. Whereas the reanalysed data from Nentwig & Wissel (1986) only includes spiders preying on nondangerous prey, the size difference between predators largely explains who eats whom (Wise, 2006). Finally, we found that, when prey is small relative to the spider's size, active-hunting spiders have a higher frequency of successful predation events. This result suggests that active-hunting spiders are better than sit-and-wait spiders at subduing prey that is smaller than them.

Our results for spiders are likely generalizable to other taxa. For instance, sit-and-wait and active-hunting behaviour occurs in different species of fish, amphibians

and reptiles (Schoener, 1971; Huey & Pianka, 1981; Greene, 1986), and likely a continuum of strategies from low to high mobility occurs in all predatory taxa. Differences in mobility, and thus variability in encounter rates with predators, can be also important outside the foraging-for-food context, such as during dispersal or when searching for mates. This influence of mobility on predation risk could also affect life history traits other than offspring size, that is age and size at maturation (Vollrath & Parker, 1992; De Mas *et al.*, 2009).

Higher encounter rates with predators generally lead to selection favouring larger spiderlings. In contrast, higher predation rates on *eggs* (before they hatch) could favour smaller offspring. For example, small eggs can develop faster and hatch earlier, avoiding predators that appear later in the season (Kudo, 2001). Similarly, females producing small eggs can have higher fecundity, potentially diluting predation risk. However, this type of selection is unlikely to occur widely in spiders, as a previous study found no relationship between egg size and maternal care (i.e. sitting with the egg sac until hatching, which should decrease exposure of the eggs to predation) (Simpson, 1995). Therefore, the most parsimonious explanation for our results is that the post-hatching encounter rate with predators, which is a function of the mobility associated with each foraging mode, strongly drives selection on egg size. More information on the mobility of animals and optimal attack rates as a function of predator/prey body-size ratio could help disentangle the causes of egg-size evolution and improve the accuracy of our predictions.

One unexpected result from our data analysis is that as female size increased, both egg size and egg number became more similar between the two foraging modes (i.e. the statistically significant 'body size  $\times$  foraging mode' interaction, Fig. 2). We propose three nonmutually exclusive explanations for this interaction. First, smaller active-hunting species and, more importantly, their immature stages could be more vulnerable relative to the larger active-hunting species (Fox & Czesak, 2000). Hence, larger egg sizes could be more strongly favoured for the smaller active-hunting species. In addition, a lower difference in body size between mother and hatchling can substantially reduce the developmental time of the offspring, which would decrease their time exposed to predators before reaching adulthood (Fox, 1994; Gillooly *et al.*, 2002). Such an advantage would not exist for sit-and-wait predators which, due to their lower mobility, encounter fewer predators. A second explanation could be differences in predominant dispersal mode between spiders of different body size and foraging mode. In both sit-and-wait and active-hunting spiders, long-distance dispersal is usually accomplished by ballooning – floating in the air and riding the wind on spider-made silken 'kites' – which is favoured by smaller body size (Roff, 1991; Suter, 1999). For small sit-and-wait females, ballooning could be

more frequent as a dispersal mode for their offspring, and thus, a relatively small body size is favoured compared to offspring of active-hunting spiders. Moreover, as ballooning is a highly stochastic dispersal mechanism (e.g. landing on one or another habitat depends on the strength and direction of the wind), high fecundity would be favoured (Duarte & Alcaraz, 1989). As the size of sit-and-wait females, and thus that of their offspring, increases (Hendriks & Mulder, 2008), other dispersal modes (e.g. bridging running upside-down on silk bridges; Moya-Laraño *et al.*, 2008) may become more important, thereby favouring larger offspring for sit-and-wait spiders independently of foraging consequences. Finally, it could be that the largest active-hunting spiders are not able to produce larger offspring because offspring size is physiologically constrained by the size of the mother, and females cannot produce offspring larger than some threshold (Hendriks & Mulder, 2008).

Another unanticipated result is that the relationship between female size and both egg size and clutch size differed between the data sets from the two biogeographic areas studied (i.e. the significant interaction between prosoma  $\times$  biogeographic area in Table 3). These two data sets come not only from different biogeographic regions with different climates, but are samples from two vastly different expanses of area (the small state of Connecticut, USA, in Kaston, 1981 vs. the entire Australian continent in Mascord, 1970). We thus expect that differences in climate (e.g. Connecticut is much colder in winter), and the large differences in geographic surface area, have led to diverse sources of selective pressures that could explain the observed differences in allometric relationships. This possibility suggests the potential insights to be gained by future biogeographic research on the relationship between clutch size, egg size and female size. As the interaction with region was included in our model, our results are not confounded by these regional differences.

The difference in body size between predator and prey has a larger effect on predation success for active predators than for sit-and-wait predators due to differences in foraging strategies. This difference in the importance of body-size differences led us to predict that highly mobile predators should lay larger but fewer eggs than less mobile (i.e. sit-and-wait) predators when these generalist predators are considered in the context of the food webs in which they are embedded, and mainly due to the effects of intra-guild predation. We tested the prediction across spider species and found that, when compared with active-hunting spiders, sit-and-wait foragers lay smaller eggs but higher numbers of eggs per clutch. Clearly, ecological networks (both mutualistic – e.g. pollination networks – and antagonistic – e.g. food webs) include diverse sources of selection that can affect the

evolution of life history traits, a subject that deserves further investigation.

## Acknowledgments

We thank S. Magalhães, M.A. Rodríguez-Gironés, A.L. Llandres, D. Sol, M. Riba, J. Piñol, J.M. Montoya, C. Mulder and one anonymous reviewer for their useful comments on the manuscript, and J. Fox for guidance in the incorporation of effects in plots from PGLS models. OVV was supported by a scholarship from the Ministerio de Ciencia e Innovación of the Spanish Government (BES-2008-004515). This research was supported by grants CGL2007-60520 and CGL2010-18602 to JML.

## References

- Agnarsson, I. 2003. The phylogenetic placement and circumscription of the genus *Synotaxus* (Araneae: Synotaxidae), a new species from Guyana, and notes on theridioid phylogeny. *Invertebr. Syst.* **17**: 719–734.
- Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). *Zool. J. Linn. Soc.* **141**: 447–626.
- Agnarsson, I. 2006. A revision of the New World *ximius* lineage of *Anelosimus* (Araneae, Theridiidae) and a phylogenetic analysis using worldwide exemplars. *Zool. J. Linn. Soc.* **146**: 453–593.
- Arnedo, M.A., Coddington, J., Agnarsson, I. & Gillespie, R.G. 2004. From a comb to a tree: phylogenetic relationships of the comb-footed spiders (Araneae, Theridiidae) inferred from nuclear and mitochondrial genes. *J. Mol. Evol.* **31**: 225–245.
- Arnedo, M.A., Agnarsson, I. & Gillespie, R.G. 2007. Molecular insights into the phylogenetic structure of the spider genus *Theridion* (Araneae, Theridiidae) and the origin of the Hawaiian Theridion-like fauna. *Zool. Scr.* **36**: 337–352.
- Bascompte, J. 2009. Disentangling the web of life. *Science* **325**: 416–419.
- Benjamin, S.R. 2004. Taxonomic revision and phylogenetic hypothesis for the jumping spider subfamily Ballinae (Araneae, Salticidae). *Zool. J. Linn. Soc.* **142**: 1–82.
- Blaustein, L. 1997. Non-consumptive effects of larval Salamandra on crustacean prey: can eggs detect predators? *Oecologia* **110**: 212–217.
- Bosselaers, J. & Jocque, R. 2000. Hortipes, a huge genus of tiny Afrotropical spiders (Araneae, Liocranidae). *Bull. Am. Mus. Nat. Hist.* **256**: 4–108.
- Bosselaers, J. & Jocque, R. 2002. Studies in Corinnidae: cladistic analysis of 38 corinnid and liocranid genera, and transfer of Phrurolithinae. *Zool. Scr.* **31**: 241–270.
- Brose, U., Ehnes, R.B., Rall, B.C., Vucic-Pestic, O., Berlow, E.L. & Scheu, S. 2008. Foraging theory predicts predator-prey energy fluxes. *J. Anim. Ecol.* **77**: 1072–1078.
- Coddington, J.A. 2005. Phylogeny and classification of spiders. In: *Spiders of North America: An Identification Manual* (D. Ubick, P. Paquin, P.E. Cushing & V. Roth, eds), pp. 18–24. American Arachnological Society, USA.

- De Mas, E., Ribera, C. & Moya-Laraño, J. 2009. Resurrecting the differential mortality model of sexual size dimorphism. *J. Evol. Biol.* **22**: 1739–1749.
- Duarte, C.M. & Alcaraz, M. 1989. To produce many small or few large eggs: a size-independent reproductive tactic of fish. *Oecologia* **80**: 401–404.
- Fang, K., Yang, C.C., Lue, B.W., Chen, S.H. & Lue, K.Y. 2000. Phylogenetic corroboration of superfamily Lycosoidae spiders (Araneae) as inferred from partial mitochondrial 12S and 16S ribosomal DNA sequences. *Zool. Stud.* **39**: 107–113.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.
- Fox, C.W. 1994. The influence of egg size on offspring performance in the seed beetle, *Callosobruchus maculatus*. *Oikos* **71**: 321–325.
- Fox, J. 2003. Effect displays in R for generalised linear models. *J. Stat. Softw.* **8**: 1–9.
- Fox, C.W. & Czesak, M.E. 2000. Evolutionary ecology of progeny size in arthropods. *Annu. Rev. Entomol.* **45**: 341–369.
- Garb, J.E., Gonzalez, A. & Gillespie, R.G. 2004. The black widow spider genus *Latrodectus* (Araneae: Theridiidae): phylogeny, biogeography, and invasion history. *J. Mol. Evol.* **31**: 1127–1142.
- Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M. & Brown, J.H. 2002. Effects of size and temperature on developmental time. *Nature* **417**: 70–73.
- Gomez, J.M., Abdelaziz, M., Camacho, J.P.M., Munoz-Pajares, A.J. & Perfectti, F. 2009. Local adaptation and maladaptation to pollinators in a generalist geographic mosaic. *Ecol. Lett.* **12**: 672–682.
- Grafen, A. 1989. The phylogenetic regression. *Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci.* **326**: 119–157.
- Greene, C.H. 1986. Patterns of prey selection: implications of predator foraging tactics. *Am. Nat.* **128**: 824–839.
- Griswold, C.E., Coddington, J.A., Hormiga, G. & Scharff, N. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbicularia: Deinopoidea, Araneoidea). *Zool. J. Linn. Soc.* **123**: 1–99.
- Griswold, C.E., Coddington, J.A., Platnick, N.I. & Forster, R.R. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). *J. Arachnol.* **27**: 53–63.
- Hart, M.W. 2008. Speciose versus species-rich. *Trends Ecol. Evol.* **23**: 660–661.
- Hawkeswood, T.J. 2003. *Spiders of Australia: An Introduction to Their Classification, Biology and Distribution*. Pensoft, Sofia, Bulgaria.
- Heath, D.D., Heath, J.W., Bryden, C.A., Johnson, R.M. & Fox, C.W. 2003. Rapid evolution of egg size in captive salmon. *Science* **299**: 1738–1740.
- Hedin, M.C. & Maddison, W.P. 2001. A combined molecular approach to phylogeny of the lumping spider subfamily Dendryphantinae (Araneae: Salticidae). *J. Mol. Evol.* **18**: 386–403.
- Hendriks, A.J. & Mulder, C. 2008. Scaling of offspring number and mass to plant and animal size: model and meta-analysis. *Oecologia* **155**: 705–716.
- Hormiga, G. 2000. *Higher Level Phylogenetics of Erigonine Spiders (Araneae, Linyphiidae, Erigoninae)*. Smithsonian Institution Press, Washington, DC.
- Huey, R.B. & Pianka, E.R. 1981. Ecological consequences of foraging mode. *Ecology* **62**: 991–999.
- Jones, M., Laurila, A., Peuhkuri, N., Piironen, J. & Seppa, T. 2003. Timing an ontogenetic niche shift: responses of emerging salmon alevins to chemical cues from predators and competitors. *Oikos* **102**: 155–163.
- Kaston, B.J. 1981. *Spiders of Connecticut*. State Geological and Natural History Survey of Connecticut, Hartford, CT.
- Kudo, S. 2001. Intraclutch egg-size variation in acanthosomatid bugs: adaptive allocation of maternal investment? *Oikos* **92**: 208–214.
- Laurila, A., Pakkasmaa, S., Crochet, P.A. & Merila, J. 2002. Predator-induced plasticity in early life history and morphology in two anuran amphibians. *Oecologia* **132**: 524–530.
- Levi, H.W. 2002. Keys to the genera of Araneid orbweavers (Araneae, Araneidae) of the Americas. *J. Arachnol.* **30**: 527–562.
- Lima, S.L. & Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.-Rev. Can. Zool.* **68**: 619–640.
- Maddison, W.P. & Hedin, M.C. 2003. Jumping spider phylogeny (Araneae: Salticidae). *Invertebr. Syst.* **17**: 529–549.
- Maddison, W.P. & Maddison, D.R. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. <http://mesquiteproject.org>.
- Maddison, D.R. & Schulz, K.-S. 2007. The tree of life web project. Retrieved 02 December 2013, from <http://tolweb.org>.
- Magalhães, S., Janssen, A., Montserrat, M. & Sabelis, M.W. 2005. Prey attack and predators defend: counterattacking prey trigger parental care in predators. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **272**: 1929–1933.
- Martins, E.P. 1996. Conducting phylogenetic comparative studies when the phylogeny is not known. *Evolution* **50**: 12–22.
- Mascord, R. 1970. *Australian Spiders in Colour*. Charles E. Tuttle, Rutland, UK.
- Miller, J.A. & Hormiga, G. 2004. Clade stability and the addition of data: a case study from erigonine spiders (Araneae: Linyphiidae, Erigoninae). *Cladistics* **20**: 385–442.
- Miller, J.R., Ament, J.M. & Schmitz, O.J. 2014. Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *J. Anim. Ecol.* **83**: 214–222.
- Moore, R.D., Newton, B. & Sih, A. 1996. Delayed hatching as a response of streamside salamander eggs to chemical cues from predatory sunfish. *Oikos* **77**: 331–335.
- Moya-Laraño, J. 2010. Can temperature and water availability contribute to the maintenance of latitudinal diversity by increasing the rate of biotic interactions? *Open Ecol. J.* **3**: 1–13.
- Moya-Laraño, J. 2012. O matrices and eco-evolutionary dynamics. *Trends Ecol. Evol.* **27**: 139–140.
- Moya-Larano, J., Roman Bilbao-Castro, J., Barrionuevo, G., Ruiz-Lupion, D., Casado, L.G., Montserrat, M. et al. 2014. Eco-evolutionary spatial dynamics: rapid evolution and isolation explain food web persistence. *Adv. Ecol. Res.* **50**: 75–143.
- Moya-Laraño, J., Vinkovic, D., De Mas, E., Corcobado, G. & Moreno, E. 2008. Morphological evolution of spiders predicted by pendulum mechanics. *PLoS ONE* **3**: e1841.
- Moya-Laraño, J., Verdén-Vilalta, O., Rowntree, J., Melguizo-Ruiz, N., Montserrat, M. & Laiolo, P. 2012. Climate change and eco-evolutionary dynamics in food webs. *Adv. Ecol. Res.* **47**: 1–80.
- Moya-Laraño, J., Foellmer, M.W., Pekár, S., Arnedo, M.A., Bilde, T. & Lubin, Y.D. 2013. Evolutionary Ecology: linking



- traits, selective pressures and ecological functions. In: *Spider Research in the 21st Century: Trends and Prospects* (D. Penney, ed.), pp. 112–153. Siri Scientific Press, Manchester.
- Murphy, N.P., Framenau, V.W., Donnellan, S.C., Harvey, M.S., Park, Y.C. & Austin, A.D. 2006. Phylogenetic reconstruction of the wolf spiders (Araneae: Lycosidae) using sequences from the 12S rRNA, 28S rRNA, and NADH1 genes: Implications for classification, biogeography, and the evolution of web building behavior. *J. Mol. Evol.* **38**: 583–602.
- Nentwig, W. & Wissel, C. 1986. A comparison of prey lengths among spiders. *Oecologia* **68**: 595–600.
- Paine, R.T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-pisaster* interaction. *Ecology* **57**: 858–873.
- Paradis, E. 2006. *Analysis of Phylogenetics and Evolution with R*. Springer, New York.
- Petranka, J.W., Sih, A., Kats, L.B. & Holomuzki, J.R. 1987. Stream drift, size-specific predation, and the evolution of ovum size in an amphibian. *Oecologia* **71**: 624–630.
- Prenter, J., Montgomery, W.I. & Elwood, R.W. 1997. Sexual dimorphism in northern temperate spiders: implications for the differential mortality model. *J. Zool.* **243**: 341–349.
- Prenter, J., Elwood, R.W. & Montgomery, W.I. 1998. No association between sexual size dimorphism and life histories in spiders. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **265**: 57–62.
- Purvis, A. & Garland, T. 1993. Polytomies in comparative analyses of continuous characters. *Syst. Biol.* **42**: 569–575.
- R Core Team 2014. *R: A Language and Environment for Statistical Computing*. R Core Team, Vienna, Austria.
- Roff, D.A. 1991. Life history consequences of bioenergetic and biomechanical constraints on migration. *Amer. Zool.* **31**: 205–215.
- Scharff, N. & Coddington, J.A. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zool. J. Linn. Soc.* **120**: 355–434.
- Schmitz, O.J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* **319**: 952–954.
- Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**: 671–675.
- Schoener, T.W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**: 369–404.
- Sih, A. & Moore, R.D. 1993. Delayed hatching of salamander eggs in response to enhanced larval predation risk. *Am. Nat.* **142**: 947–960.
- Simpson, M.R. 1995. Covariation of spider egg and clutch size: the influence of foraging and parental care. *Ecology* **76**: 795–800.
- Smith, C.C. & Fretwell, S.D. 1974. Optimal balance between size and number of offspring. *Am. Nat.* **108**: 499–506.
- Suter, R.B. 1999. An aerial lottery: the physics of ballooning in a chaotic atmosphere. *J. Arachnol.* **27**: 281–293.
- Vollrath, F. & Parker, G.A. 1992. Sexual dimorphism and distorted sex-ratios in spiders. *Nature* **360**: 156–159.
- Werner, E.E. & Anholt, B.R. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.* **142**: 242–272.
- Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge, UK, pp. 328.
- Wise, D.H. 2006. Cannibalism, food limitation, intraspecific competition and the regulation of spider populations. *Annu. Rev. Entomol.* **51**: 441–465.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. *et al.* 2005. Body size in ecological networks. *Trends Ecol. Evol.* **20**: 402–409.

Received 10 September 2014; revised 11 April 2015; accepted 13 April 2015