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Insects from the grazing food web favoured the evolutionary habitat shift to bright environments in araneoid spiders

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The Araneoidea comprises a diverse group of web-building spiders, and part of this diversity is believed attributable to habitat expansion to bright environments. We clarified the fitness-related advantages of living in such environments by examining prey availability and the growth rates of 10 species in three families inhabiting grassland (bright) and forest understory (dim) habitats. Spiders in the grassland habitat captured more prey, derived mainly from the grazing food web, than those in the forest-floor environment, and this difference was manifested in their growth rate. Independent contrasts indicated that increased utilization of insects from the grazing food web led to an evolutionary increase in adult body size. These results suggest that the shift to bright environments enabled araneoid spiders to evolve diverse life-history traits, including rapid growth and large size, which were not possible in dim environments.

Keywords: web spider; herbivore insects; comparative method

1. INTRODUCTION

Spiders rank seventh among all animal species in global diversity (Craig 2003). Among them, the araneoid spiders that build various types of webs include roughly 28% of all species (Platnick 2005), despite the clade's relatively recent appearance. It is remarkable that the Araneoidea contains 32 times more species than its sister clade, the Deinopoidea (Craig *et al.* 1994; Bond & Opell 1998). The ancestral habitat of Orbiculariae (Araneoidea+Deinopoidea) was thought to be dark or dim environments, but some derived species shifted their habitats to bright environments, which was achieved by changing the spectral reflectance of silk, making it invisible to flying insects (Craig *et al.* 1994; Bond & Opell 1998). This habitat expansion, accompanied by the change in silk characteristics, is believed in part to have contributed to the adaptive radiation in araneoid spiders (Bond & Opell 1998).

A possible advantage of living in bright environments is that these habitats offer increased prey availability to spiders. Shimazaki & Miyashita (2005) found that the biomass of aerial insects was greater in grassland than in forest, reflecting the greater abundance of large insects belonging to the grazing food web, such as bees, grasshoppers and bugs. Therefore, we hypothesized that the shift to bright environments benefited spiders via the increased biomass of available prey in the grazing food web, and that this was a major force driving the shift from woodland environment in araneoid spiders.

Several fitness advantages exist in acquiring more food, e.g. increased survivorship, shortened generation time through shortened developmental time and increased fecundity through increased adult body size. Our hypothesis and background data led to the following specific predictions. First, spiders in the grassland environment should capture more prey and have higher growth rates than those in the forest-floor habitat. Second, most of the variation in the total prey capture rate and growth rate is explained by the variation in prey from the grazing food web. Third, large adult body size evolved in response to the increased utilization of prey from the grazing food web. To test these predictions, we examined the prey capture rate and body size in nine araneoid and one deinopoid orb-web species. Since the last prediction is concerned with an evolutionary hypothesis, we conducted a comparative, phylogenetic analysis using an independent contrast to test for an evolutionary association between the adult body size and utilization of grazing prey.

2. MATERIAL AND METHODS

The field study was conducted in a Japanese cedar (*Cryptomeria japonica*) forest and in an adjacent grassland area in southern Chiba Prefecture, eastern Japan (35°06′ N, 140°06′ E), which is a warm-temperate forest region. Japanese cedar forest is common in this region and has a high species richness of understory plants, as well as web spiders. In the grassland, the predominant plant species were the grass *Miscanthus sinensis* and the herb *Solidago altissima*, but pioneer tree species also occurred that could provide web support for large spiders.

We examined the prey capture rates of nine araneoid and one deinopoid spider species (figure 1). Because *Nephila clavata* inhabited both habitats, we treated the two populations separately. The phylogeny is based on Levi (1983) and Scharff & Coddington (1997). All these species were mainly diurnal hunters (Miyashita 1997; Watanabe 2001; Shimazaki & Miyashita 2005). Although *Eriophora transmarina* is known to be a nocturnal hunter, the two Japanese congeneric species always sit at the hub of the orb-web during daytime and capture prey.

To estimate prey capture rates, we collected prey that were caught in spider webs or in the process of being eaten by the spiders. Individual webs were visited every 45–60 min from 08.00 to 17.00 h, and the insects caught by the spiders were collected carefully using forceps. Observations were conducted 5–10 days per month, ranging from May to September. The number of individual webs visited per day varied among species (6–40; see electronic supplementary material). Prey were identified to the level of family, and to lower levels when necessary, and classified as members of the grazing or detrital web using references (see appendix in Shimazaki & Miyashita (2005)). The prey capture rate was expressed as the mean prey weight per individual visitation to a web. To compare prey biomass among spiders with different body sizes, the prey capture rate was divided by (spider mass)$^{0.7}$ for each spider species, hereafter called the 'standardized prey mass'. The value of 0.7 is a general allometric value relating body weight to metabolic rate in spiders (Peters 1983).

The body length (cephalothorax–abdomen length) of each spider observed was measured at the time of prey observations. The index of spider body mass was expressed as (body length)$^{2.4}$, since the body weights of four araneoid species showed an allometric

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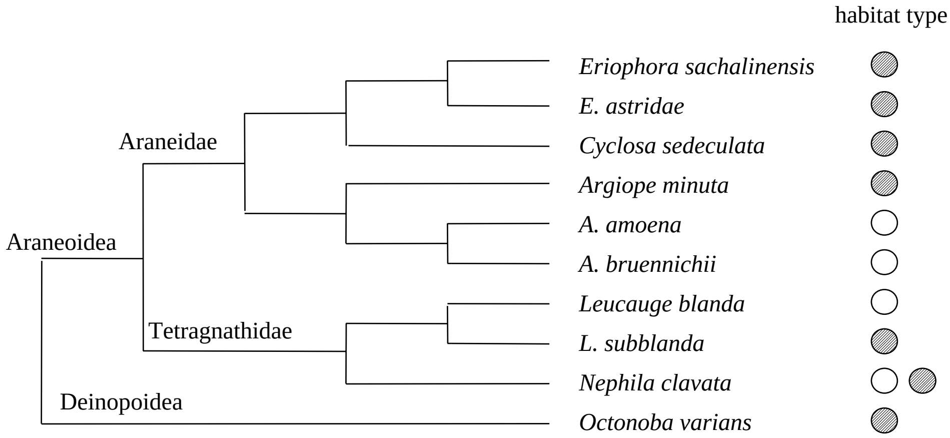

Figure 1. Phylogeny of spiders examined in this study. Open and shaded circles represent bright and dim environments where spiders inhabit, respectively.

value (slope) of about 2.4 with respect to body length (Miyashita 1992, 1999). The growth rate (GR) for each spider population was represented using the formula $\text{GR}=(W_{t+k}-W_t)/W_m 0.7/k$, where W_{t+k} and W_t are the mean estimated body weight for each species in $t+k$ and t months, respectively, and W_m is the average of W_{t+k} and W_t. Although logarithmic transformation of body weight is often used for estimating growth rate, it implicitly assumes an allometric value of 1. This is unsuitable for comparing the relative growth rates of species with different body weights because body weight increases at around $(\text{weight})^{0.7}$ (Peters 1983).

Both the prey capture rate and the growth rate of species living in different environments (forest versus grassland) were compared by an independent *t*-test using mean values of each species (or population). Additionally, comparisons accounting for the difference in web traits were performed by an ANOVA for the prey capture and a paired *t*-test for the growth, which included taxon (*Nephila*, *Leucauge* and *Argiope*) as a covariate. (A paired *t*-test was used for the growth rate because only a single value was estimated for each species.) For *Argiope* in the grassland, the average of the two species was used for the paired *t*-test. A simple regression analysis was conducted to determine whether prey from the grazing food web explained the variation in the total prey biomass better than those from the detritus food web. A simple regression analysis was also performed to see if the growth rate reflected the ratio of grazing and detrital prey biomasses (hereafter called the GD ratio). We did not consider the effect of phylogeny for these two analyses, as the GD ratio is not affected by phylogeny (Shimazaki & Miyashita 2005). Finally, we performed an independent contrast analysis using comparative analysis by independent contrasts (Purvis & Rambaut 1995) to test whether the increase in the dependency on the grazing food web led to an evolutionary increase in the adult body size of spiders. This analysis uses the differences in a given trait between two pairs of species or higher nodes to control the statistical problems arising from species relatedness. The regression through the origin was used to test the relationship between the contrasts of the GD ratio and body size. This analysis excluded *Leucauge blanda*, as it has multiple generations per year.

3. RESULTS

The standardized prey mass captured by spiders was significantly higher in the grassland habitat than in the forest-floor habitat when the data from all species were used (grassland: 11.3±3.6, forest: 4.1±1.3; $t_9=2.28$, $p=0.049$). ANOVA accounting for phylogeny showed a similar result ($F_{1,12}=9.60$, $p=0.01$); *Nephila*, *Leucauge* and *Argiope* in the grassland captured 3.6, 9.5 and 20.1 times more prey biomass, respectively (table 1). Total prey mass was strongly related to the prey mass of the grazing food web ($F_{1,9}=68.6$, $p<0.001$, $r^2=0.884$; figure 2*a*), while it had no relationship with the detrital prey mass ($F_{1,9}=0.6$, $p=0.441$). Therefore, the variation in prey mass was mostly attributable to that in prey from the grazing food web.

Table 1. Prey capture rate (s.e.) and growth rate of three groups of spiders inhabiting two habitats. (As described in the text, both values are dimensionless standardized by allometry of body size. The growth rate has no s.e. because it is a single estimate.)

spider genus	prey capture rate		growth rate	
	grassland	forest	grassland	forest
Nephila	7.34 (3.88)	1.99 (0.73)	4.08	3.39
Argiope	14.11 (5.96)	0.68 (0.18)	6.16	3.02
Leucauge	3.80 (0.44)	0.39 (0.09)	3.29	2.09

Spiders inhabiting the grassland grew twice as fast as those in the forest, though not significantly (grassland: 4.9±1.1, forest: 2.4±0.5; $t_6=2.15$, $p=0.075$). The paired *t*-test accounting for phylogeny did not show a clear difference either ($t_2=2.98$, $p=0.097$), but *Nephila*, *Leucauge* and *Argiope* in the grassland grew 1.2, 1.6 and 2.1 times faster than conspecifics or congeners in the forest habitat, respectively (table 1). This ranking was very similar to that found in prey biomass. Regression analysis showed that growth rate was positively related to the GD ratio ($F_{1,6}=7.1$, $p=0.038$; figure 2*b*), supporting the hypothesis that the prey mass from the grazing food web contributed to the rapid growth of spiders.

A significantly positive evolutionary relationship was observed between the increment in the GD ratio (x) and that of the body size (y) ($F_{1,7}=16.8$, $p=0.005$), and the regression through the origin was $y=0.226x$ (figure 2*c*). This implies that there was an evolutionary trend towards larger adult body size with increasing dependence on prey in the grazing food web.

4. DISCUSSION

We demonstrated that the prey biomass of spiders in the grassland was greater than that in the forest-floor habitat, and this difference was correlated with increases in the growth rates of spiders, both within and among species. Moreover, most of the variation in the prey biomass among spider species was explained by the variation in the prey biomass from the grazing food web (88%). These results support our hypothesis that the increased prey availability in the grazing food web in

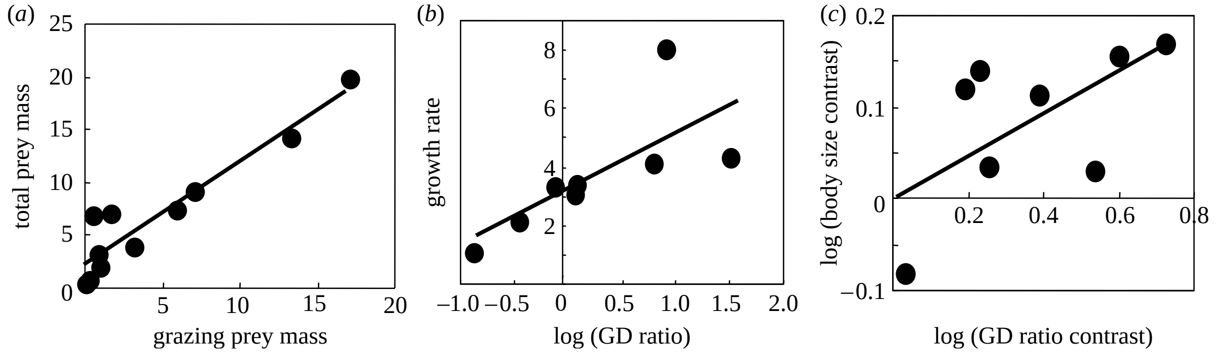

Figure 2. Relationships between (*a*) biomass of prey from the grazing food web and total biomass of prey, (*b*) GD ratio and spider growth rate and (*c*) increment of the GD ratio and that of the adult body size of spiders. Details are described in the text.

bright environments enhanced the level of total prey availability for spiders, which then enabled spiders to grow faster. This scenario appears to be general and widespread because sunlight is a limiting factor for terrestrial primary production (e.g. Begon *et al.* 2005), leading to a greater biomass of grazers in bright environments.

At least three potential advantages exist in growing faster: enhanced individual fecundity through increased body size, increased number of generations per growing season and increased survivorship owing to the shortening of the vulnerable juvenile period. All these could be seen in spiders as ecological and evolutionary responses, but we focused on evolutionary perspectives because our objective was to identify the force driving the evolutionary habitat shift, and the interspecific variation in life-history traits is generally much greater than the intraspecific variation (e.g. Craig 1987). The independent contrast revealed an evolutionary tendency towards increased adult female body size with increasing utilization of prey from the grazing food web. This suggests a predominance of fecundity selection over viability selection in those species that shifted their habitats to bright environments. An increased number of generations, another possible advantage, was seen in *L. blanda*, which was not included in the body size analysis. Although the body sizes of *L. blanda* and forest dwelling *Leucauge subblanda* were similar (Shimazaki & Miyashita 2005), the former has at least two generations annually, while the latter is univoltine. Since *L. blanda* grew 1.6 times faster than *L. subblanda*, the difference in development time probably contributed to the higher generation turnover in *L. blanda*. The survivorship advantage in bright environments remains unclear, but the benefit of the shorter developmental period might be offset by a higher predation rate because habitats with abundant prey often have a higher predator density (e.g. Riechert & Hedrick 1990).

Our results demonstrated that the shift to bright environments had the potential to broaden life-history characteristics in araneoid spiders, which appeared to be realized by the utilization of food resources not available to ancestral spiders. However, living in bright environments is not always beneficial to spiders owing to the greater heat stress and risk of desiccation (Tolbert 1979), as well as the greater predation pressure. Further research on the evolutionary association between life-history and physiological traits and habitat characteristics is necessary using a wide range of araneoid and deinopoid spiders.

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Begon, M., Townsend, C. R. & Harper, J. L. 2005 *Ecology: from individuals to ecosystems*, 4th edn. Malden, MA: Blackwell Publishing.

Bond, J. E. & Opell, B. D. 1998 Testing adaptive radiation and key innovation hypotheses in spiders. *Evolution* **52**, 403–414. (doi:10.2307/2411077)

Craig, C. L. 1987 The significance of spider size to the diversification of spider-web architectures and spider reproductive modes. *Am. Nat.* **129**, 47–68. (doi:10.1086/284622)

Craig, C. L. 2003 *Spiderwebs and silk: tracing evolution from molecules to genes to phenotypes*. Oxford, UK: Oxford University Press.

Craig, C. L., Bernard, G. D. & Coddington, J. A. 1994 Evolutionary shifts in the spectral properties of spider silks. *Evolution* **48**, 287–296. (doi:10.2307/2410093)

Levi, H. W. 1983 The orb-weaver genera *Argiope*, *Gea*, and *Neogea* from the western pacific region (Araneae: Araneidae, Argiopinae). *Bull. Mus. Comp. Zool.* **150**, 247–338.

Miyashita, T. 1992 Variability in food consumption rate of natural populations in the spider, *Nephila clavata*. *Res. Popul. Ecol.* **34**, 15–28.

Miyashita, T. 1997 Factors affecting the difference in foraging success in three co-existing *Cyclosa* spiders. *J. Zool.* **242**, 137–149.

Miyashita, T. 1999 Life-history variation in closely related generalist predators living in the same habitat: a case study with three *Cyclosa* spiders. *Funct. Ecol.* **13**, 307–313. (doi:10.1046/j.1365-2435.1999.00318.x)

Peters, R. H. 1983 *The ecological implications of body size*. Cambridge, UK: Cambridge University Press.

Platnick, N. I. 2005 The World Spider Catalog. Ver. 6.0. http://research.amnh.org/entomology/spiders/catalog/INTRO1.html.

Purvis, A. & Rambaut, A. 1995 Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *CABIOS* **11**, 247–251.

Riechert, S. E. & Hedrick, A. V. 1990 Levels of predation and genetically based anti-predatory behavior in the spider, *Agelenopsis aperta*. *Anim. Behav.* **40**, 679–687. (doi:10.1016/S0003-3472(05)80697-9)

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. (doi:10.1006/zjls.1996.0084)

Shimazaki, A. & Miyashita, T. 2005 Variable dependence on detrital and grazing food webs by generalist predators: aerial insects and web spiders. *Ecography* **28**, 485–494. (doi:10.1111/j.0906-7590.2005.04105.x)

Tolbert, W. W. 1979 Thermal stress of the orb-weaving spider *Argiope trifasciata*. *Oikos* **32**, 386–392.

Watanabe, T. 2001 Effects of web design on the prey capture efficiency of the uloborid spider *Octonoba sybotides* under abundant and limited prey conditions. *Zool. Sci.* **18**, 585–590. (doi:10.2108/zsj.18.585)