Biological Journal of the Linnean Society, 2006, **87**, 95–102. With 2 figures

Female morphology, web design, and the potential for multiple mating in *Nephila clavipes*: do fat-bottomed girls make the spider world go round?

SHAWN E. VINCENT* and SIMON P. LAILVAUX

Department of Ecology and Evolutionary Biology, 310 Dinwiddie Hall, Tulane University, New Orleans, LA 70118, USA

Received 25 May 2004; accepted for publication 1 December 2004

In animal species where females mate with multiple males, female mating success might be expected to covary with aspects of female morphology, such as size or shape. Spiders are especially interesting in this regard, as the females of several spider groups weave intricate webs that often accommodate multiple male spiders, all of whom are potential mates. Because web design is likely to be dependent on female size/shape, we use multivariate methods to assess the relationships among female morphology, web design, and reproductive ecology over a range of body sizes in the orb-weaving spider *Nephila clavipes*. Of the measured variables, only abdomen size explained a significant amount of the variation in number of males on a web, and this relationship holds even after statistically accounting for body size. Because abdomen size is an indicator of body condition in spiders, we suggest that condition is likely to be an important factor relating to potential mating success in female spiders. We found no evidence for an association between web design and number of males on a web, although our data indicate that larger females build webs that are both larger and further from the ground than those of smaller females.

ADDITIONAL KEYWORDS: condition – ecomorphology – polyandry – reproductive success.

INTRODUCTION

Polyandry (multiple matings by females with different males) is a widespread phenomenon in the animal kingdom. In some cases, the existence of polyandry is likely driven by direct benefits gained by females in the form of nuptial gifts or protection offered by males (Vahed, 1998; Arnqvist & Nilsson, 2000), while in others, males contribute little more than sperm (Simmons, 2003). Nevertheless, even if females do not profit directly, the potential fitness benefits to mating with multiple males are thought to be substantial (Jennions & Petrie, 2000; Fedorka & Mousseau, 2002). For example, multiple matings may result in male offspring of higher quality (Hosken *et al.*, 2003) or increased heterozygosity (Liersch & Schmidt-Hempel, 1998; Foerster *et al.*, 2003) relative to offspring of females that mate with fewer males.

However, while mating with several different males may be advantageous to females, mating also imposes costs (Johnstone & Keller, 2000; Herberstein, Schneider & Elgar, 2002; Chapman *et al.*, 2003). Successful females who tolerate and mate with more males might be expected to exhibit differences in condition and/or associated morphological variables (such as body size or shape) relative to unsuccessful females, in order to better endure such costs. Alternatively, males are known to exhibit preferences for larger females in several taxa (Andersson, 1994), and consequently larger females may be more likely than smaller females to obtain multiple matings. Relatively few studies, however, have examined correlations between female morphology and reproductive success in an explicitly ecological context. Here, we adopt an ecomorphological

---

*Corresponding author. Current address: Department of Ecology and Evolutionary Biology Box G.W., Brown University, Providence, RI 02912, USA. E-mail: shawn_vincent@brown.edu

approach to investigate the relationships among female morphology, web design, and number of males present in the webs of orb-weaving spiders.

Studies of the relationships between an organism's morphology and its ecology have flourished since Arnold (1983) proposed a rigorous framework for investigating the adaptive nature of morphological variation (Wainwright & Reilly, 1994; Irschick & Garland, 2001, for review). The use of ecomorphological methods in several animal taxa has taught researchers a great deal about the relationships among morphology, habitat use, performance, and, ultimately, fitness (e.g. lizards: Losos, 1990; Irschick & Losos, 1998; Herrel, Meyers & Vanhooydonck, 2001; fish: Wainwright, Bellwood & Westneat, 2002; Langerhans *et al.*, 2003; spiders: Prenter, Elwood & Montgomery, 2003; insects: Nosil & Crespi, 2004; snakes: Vincent, Herrel & Irschick, 2004).

Spiders are in many ways ideal candidates for studies of this nature, as they occur at high densities in areas of rich vegetation, occupy a diversity of habitat types, from Arctic islands to deserts (Foelix, 1996), and exhibit a range of morphological types, including several cases of extreme sexual size dimorphism (Elgar, 1991; Foelix, 1996; Hormiga, Scharff, & Coddington, 2000). Most notably, females of several spider groups also weave intricate webs, the design features of which (including variables such as inner web height, web width, and web angle relative to the ground) are likely to be as subject to selective pressures as the morphology of the organism itself (Eberhard, 1990; Blackledge, Coddington & Gillespie, 2003; Craig, 2003).

Although webs are central to spider ecology (Craig, 1986), few ecomorphological studies have incorporated web design into their analyses. This is surprising, especially given the importance of webs to the mating systems of some spider groups. Orb-web spiders, for example, are usually promiscuous, and females often accommodate several male spiders on their webs, despite frequent instances of sexual cannibalism (Elgar, 1991; Schneider & Elgar, 2001; Herberstein, Schneider & Elgar, 2002). Because larger spiders construct larger webs, and larger webs are likely to harbour many males, one might expect a relationship between female spider size and number of males on a web. Previous studies have explored the relationships between body mass and web design (Craig, 1986; Venner *et al.*, 2002), reproductive state and web design (Higgins, 1990; Sherman, 1994), body size and web height (Eberhard, 1971), and body mass and reproductive state (Vollrath, 1987; Uetz, 1992). However, no investigators have, to our knowledge, used rigorous multivariate methods to assess the relationships among morphology, web design and reproductive ecology (including number of males on the web) within a single species. Here we consider the hypothesis that number of males on a web is related to female morphology in the orb-weaving spider, *Nephila clavipes*. In particular, we test two predictions of this hypothesis: (1) larger females have more males on their webs than smaller females, and (2) larger webs harbour more males than smaller webs.

MATERIAL AND METHODS

STUDY SITE

This study took place at the Edward F. Hebert Research Center of Tulane University in Belle Chasse, Louisiana during the month of July 2003, which is near the beginning of the breeding season for *N. clavipes*. The study was conducted in a 30 × 30-m plot in a bottomlands hardwood forest. We sampled every spider that could be located within the plot. Because the various size classes of *N. clavipes* are known to segregate spatially within a habitat (Moore, 1977), with the largest adults occurring in more open areas than smaller juveniles, our plot contained both shaded as well as open areas. We were therefore able to examine the relationships among morphology, ecology, and reproductive state for a wide range of sizes. We examined morphology, web design/placement, and reproductive state for a total of 35 female *N. clavipes*, ranging in cephalothorax length from 0.16 to 0.92 cm (see Table 1).

WEB DESIGN AND REPRODUCTIVE STATE MEASUREMENTS

We recorded four measurements of web design: (1) distance of the centre of the web from the ground (± 0.1 cm); (2) maximum width of the web (± 0.1 cm) (maximum distance over which web spanned in the horizontal axis); (3) maximum height of the inner portion of the web (± 0.1 cm) (maximum distance over which web spanned in the vertical axis), and (4) web angle relative to the ground (see Fig. 1). Web linear measurements were recorded using a measuring tape. Web angle was calculated using a Speed Partz Smarttool (Speed Partz, West Chester, OH).

We dissected the abdomen of each female spider to determine whether or not they were gravid. If eggs were present, we measured the mass of each clutch using a Denver Instruments M- 220 electronic balance (± 0.01 mg). We include only clutch mass in our analyses, as number of eggs could not be accurately determined in most cases. Finally, we recorded the number of males present in each web.

MORPHOMETRICS

We made the following morphological measurements in centimetres using Mitutoyo digital calipers

Table 1. Mean values ± 1 SEM of both morphological and ecological variables recorded for 35 female *Nephila clavipes*

Variable	Mean ±1 SEM	Max	Min
Cephalothorax width (cm)	0.38 ± 0.02	0.69	0.15
Cephalothorax height (cm)	0.28 ± 0.01	0.40	0.15
Cephalothorax length (cm)	0.52 ± 0.03	0.92	0.16
Abdomen length (m)	0.98 ± 0.06	1.62	0.21
Abdomen width (cm)	0.33 ± 0.02	0.56	0.15
Abdomen height (cm)	0.33 ± 0.02	0.65	0.12
Pedipalp length (cm)	0.35 ± 0.02	0.61	0.07
Distance of web centre from ground (cm)	144.1 ± 7.74	228	69.0
Maximum web width (cm)	99.6 ± 11.6	399	12.0
Maximum inner web height (cm)	46.2 ± 4.40	109	13.0
Web angle (°)	64.7 ± 2.27	89.0	12.0
Number of males in web	1.00 ± 0.18	4.00	0.00
Mass of eggs (mg)	10.4 ± 0.30	60.0	0.00

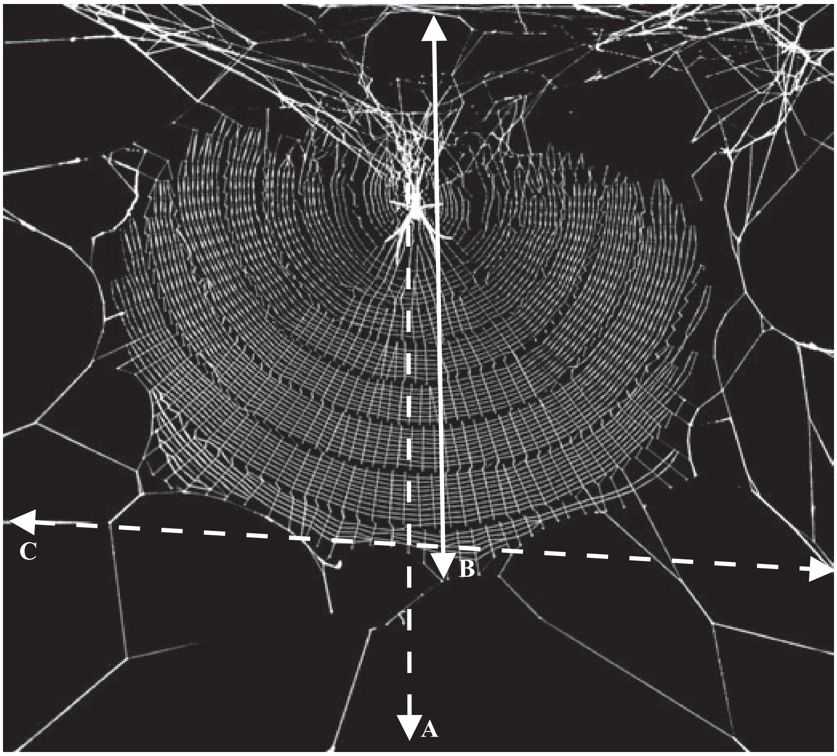

Figure 1. Measurements made on webs. A, distance of centre of web from the ground. B, maximum height of inner portion of web. C, maximum width of web. All measurements were made in centimeters. Dotted lines indicate measurements extending out of the picture, while the solid line is a real distance. Note that while this picture shows a female *Nephila senegalensis* spider and web, rather than *N. clavipes*, *N. senegalensis* and *N. clavipes* webs are superficially similar (SPL, pers. observ.). This picture is used here only to illustrate how web design was quantified. Photograph © Samuel Zschokke. Used with permission.

(± 0.01 mm): pedipalp length (total length from base to tip), cephalothorax length, cephalothorax width (widest point), cephalothorax height (highest point), abdomen length, abdomen width (widest point), and abdomen height (highest point).

STATISTICAL ANALYSIS

To meet the assumption of homoscedascity for regression techniques (Sokal & Rohlf, 1981), all variables were successfully $\log_{10}$ transformed prior to analysis,

Table 2. Reduced major axis regressions of $\log_{10}$ morphology (dependent variables) vs. $\log_{10}$ cephalothorax length (independent variable). All variables scale isometrically vs. cephalothorax length, except cephalothorax height, which exhibits significant negative allometry

Variable	Slope ±1 SEM	y-intercept ±1 SEM	95% CI	(slope)	r^2
Cephalothorax width (cm)	0.93 ± 0.04	–0.14 ± 0.01	0.83	1.02	0.92
Cephalothorax height (cm)*	0.60 ± 0.05	–0.37 ± 0.02	0.48	0.72	0.69
Abdomen length (cm)	1.12 ± 0.07	0.30 ± 0.02	0.97	1.27	0.86
Abdomen width (cm)	0.93 ± 0.06	–0.20 ± 0.02	0.79	1.07	0.81
Abdomen height (cm)	1.11 ± 0.09	–0.16 ± 0.03	0.91	1.27	0.75
Pedipalp length (cm)	1.09 ± 0.06	–0.13 ± 0.02	0.96	1.21	0.89

and the normality of the transformed data confirmed using Lillifores tests. The scaling relationships for morphological variables were analysed to determine whether body shape changes over the measured size range (Table 2). Scaling relationships were analysed by regressing cephalothorax length (independent variable) against all other $\log_{10}$ body variables using reduced major axis regression (RMA) (Sokal & Rolf, 1981). RMA was used instead of typical least squares regression in order to account for measurement error common in morphological data.

To examine the relationship between morphology and web characters, we first performed a principal components analysis in order to reduce the dimensionality of the data set. The broken stick method (Frontier, 1976; Jackson, 1993) was subsequently used to determine which principal components explained a significant portion of the variation in the data. Plots of PC1 (size) vs. web measurements are shown in Figure 2. Finally, to examine the variation in the number of males in a given web, a stepwise regression (backwards model) was performed with the $\log_{10}$ number of males in the web as the dependent variable and the $\log_{10}$ individual morphological measurements, $\log_{10}$ mass of eggs, and $\log_{10}$ web measurements as the independent variables. The resultant partial regression coefficients express the correlation between two variables under the condition that all concomitantly measured variables are held constant (Kachigan, 1991), allowing us to examine relationships between the above variables independent of body size.

We also performed an explicitly size-adjusted analysis to specifically examine whether web or body shape were significantly related to the number of males in the web. For this 'size-free' analysis, we calculated the residuals from linear least-squares regressions for $\log_{10}$ spider morphology (body measurements [*y*-axis] vs. cephalothorax length [*x*-axis]), $\log_{10}$ web measurements (web measurements [*y*-axis] vs. max web width [*x*-axis]), and $\log_{10}$ mass of eggs (mass of eggs [*y*-axis] vs. cephalothorax length [*x*-axis]). These size-free variables were subsequently used as the independent variables in a stepwise regression (backwards model), with the $\log_{10}$ number of males in a web as the lone dependent variable.

RESULTS

MORPHOLOGY

All morphological variables scale isometrically vs. cephalothorax length in *N. clavipes* (Table 2), except cephalothorax height, which exhibits significant negative allometry ($t = 8.00$, d.f. = 34, $P < 0.0001$). Hence, the overall body shape of *N. clavipes* changes little over the measured size range except in cephalothorax height, which appears to be larger, relative to body size, in smaller spiders.

The PCA performed on morphological variables yielded two axes (Table 3) that together explained 94.8% of the total variation in the data. From the loadings of the morphological variables on these two axes it is apparent that the first axis is a clear indicator of variation in body size while the second is an indicator of variation in body shape. However, the second axis explains only 4.8% of the observed variation (Table 3). Thus, while there is significant variation in body size in this sample of *N. clavipes*, there is little apparent variation in body shape indicated from both the scaling of morphological measurements (with the single exception of cephalothorax height) as well as the PCA.

RELATIONSHIPS AMONG MORPHOLOGY, WEB DESIGN, AND REPRODUCTIVE STATE

As previously noted for other orb-weaving spiders (Brown, 1981; Olive, 1982; Craig, 1987; Zschokke, 1997), web size is highly positively correlated with body size in *N. clavipes*, with both web height and web width increasing over the sampled size range (Fig. 2). Thus, larger spiders generally build overall larger webs than smaller spiders. Web angle also generally increases with overall body size in *N. clavipes* (Fig. 2).

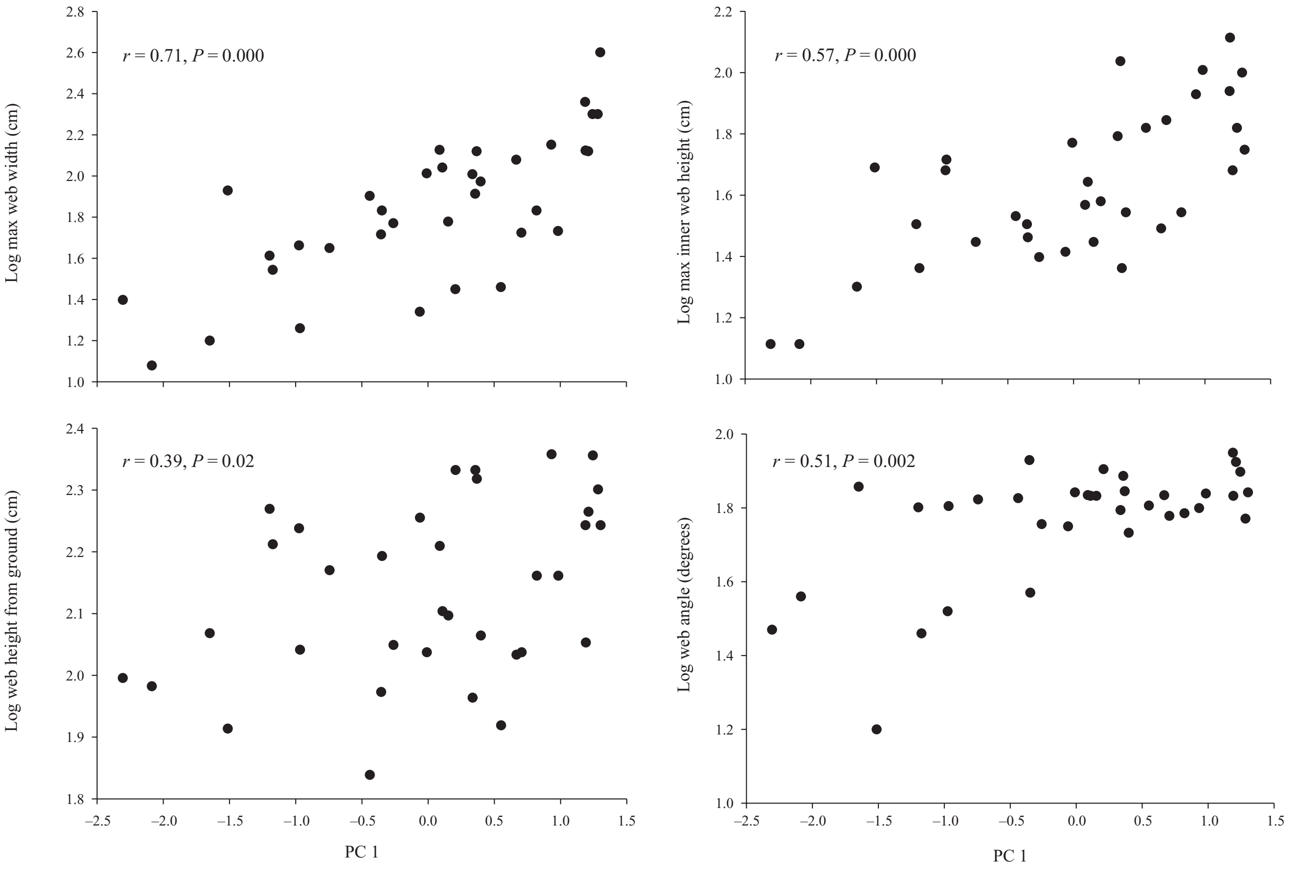

Figure 2. Plots of PC 1 vs. $\log_{10}$-transformed web measurements. All web measurements are significantly correlated with size.

Table 3. Loadings from a principal components analysis of non-size adjusted $\log_{10}$-transformed morphometric measurements. Variables loading strongly on each principal component are indicated in bold

Variable	PC1	PC2
Cephalothorax width	**0.954**	–0.200
Cephalothorax height	**0.921**	0.211
Cephalothorax length	**0.968**	–0.187
Abdomen length	**0.971**	0.004
Abdomen width	**0.966**	0.181
Abdomen height	**0.927**	0.304
Pedipalp length	**0.936**	–0.302
Eigenvalue	6.306	0.336
% variation explained	90.0	4.800

However, although very large spiders almost exclusively constructed webs 90 ° relative to the ground (Fig. 2), there is substantial variation in web angle over the sampled size range. As a result, while larger spiders typically build webs perpendicular relative to the ground, smaller individuals vary their web orientation to the ground considerably, with no pattern evident.

From the non-size adjusted stepwise regression model of number of males in the web, the model produced included abdomen width ($\beta = 0.93$, $P < 0.0001$), and abdomen height ($\beta = 0.63$, $P < 0.0001$). These beta coefficients allow us to assess the relative importance of the variables in the model (Kachigan, 1991), and a comparison of the two values (i.e. taking the ratio of the squares of the beta coefficients) reveals that abdomen width accounts for roughly twice as much of the variance in number of males as does abdomen height. Moreover, the model was highly significant ($R = 0.74$, $r^2 = 0.53$, $P < 0.0001$). Therefore, females with wider and taller abdomens relative to other females in this sample have significantly more males in their webs. The size-adjusted model only retained abdomen height ($\beta = 0.33$, $P < 0.05$), but the overall model was still significant ($R = 0.33$, $r^2 = 0.12$, $P < 0.05$). Thus, abdomen height – independent of body size – was significantly correlated with the number of males in a female's web.

DISCUSSION

We predicted positive relationships between number of males on a web and two aspects of *N. clavipes* ecomorphology: female size and web size. Whereas our first prediction was supported, with overall abdomen size explaining a significant amount of the variation in number of males on a web, our second prediction regarding web size was not, despite a correlation between web size and body size. Thus, while larger spiders build bigger webs, consistent with previous findings in other orb-weavers (Brown, 1981; Olive, 1982; Craig, 1986, 1987; Eberhard 1989, 1990), these larger webs do not necessarily harbour more males. Indeed, multiple regression analyses performed on size-corrected variables show that abdomen height is the only statistically significant predictor of number of males on a web in our sample once body size has been accounted for. Female size, and abdomen size in particular, therefore appears to be the most important morphological factor influencing male presence on a web.

One possible explanation for the importance of abdomen size to male presence on a web is that larger females may be more fecund (Head, 1995; Marshall & Gittleman, 1994; Prenter, Elwood & Montgomery, 1999). However, egg clutch mass did not correlate significantly with any variables in our sample, suggesting that fecundity is less important here than morphology. A more likely explanation is that overall condition of the female (i.e. size-corrected body mass) might play a role in attracting males to a particular web (Danielson-Francois *et al*., 2002). Because orb-web spiders are known to have poor vision, female mass may be easier to assess (e.g. via vibrations in the web) than female size (Suter, 1978; Foelix, 1996; Danielson-Francois, Fetterer & Smallwood, 2002). This explanation is consistent with previous reports that *N. clavipes* males alter their courtship behaviour based on female size, displaying more vigorously to larger females (Christenson *et al*., 1985) as the latter are likely to be heavier. Furthermore, females in good condition are less likely to cannibalize males (Newman & Elgar, 1991; Andrade, 1998; Schneider & Elgar, 2001), so taking up residence on the web of a female might be less risky. Interestingly, condition in spiders is evident from the shape and size of the abdomen, with small or shrunken abdomens indicating poor condition (Anderson, 1974; Taylor, Hasson & Clark, 1999). Thus, while we did not measure body condition directly in this study, we find it suggestive that the one variable we measured that is always correlated with number of males on a web is also an indicator of condition. Experimental studies aimed at investigating this relationship, perhaps in a controlled laboratory setting, would be extremely valuable.

Although we did not uncover evidence of any associations among web design variables and number of males on a web, our finding that larger spiders exhibit a shift in habitat use relative to smaller individuals is interesting in itself. Large females build webs that are both larger and further from the ground than those of smaller spiders (Fig. 2); specifically, web width increases more than 33-fold over the sampled size range, whereas the next most variable parameter, inner web height, increases less than 9-fold (Table 1). Large webs are also typically perpendicular to the ground, whereas the webs of smaller spiders exhibit substantial variation in their web angle relative to the ground. Given that overall spider shape changes little with size, with the exception of cephalothorax height, which is relatively larger in small spiders, this change in habitat usage is likely more related to size itself rather than shape. While similar microhabitat shifts have been shown to occur in several other orb-weaving spiders with increasing body size (e.g. Eberhard, 1990; Venner *et al*., 2002), it is not intuitively clear why body size should drive such a change microhabitat use in spiders. Web site has previously been implicated in determining types of prey captured (Eberhard, 1990), raising the possibility that larger spiders select sites suitable for capturing larger (or more) prey; however, our current dataset offers little insight into this phenomenon. Future studies addressing the relationship between spider morphology and web design/placement are therefore needed to elucidate these relationships more clearly.

In conclusion, we have shown a significant relationship between abdomen size of female *N. clavipes* spiders and number of males present on a web. Interestingly, this relationship persists even after body size is accounted for. In contrast to female size, male presence on a web appears to be unrelated to web design or web placement. We suggest that female body condition, in conjunction with other factors such as chemical cues, may be an important factor in assessment of females by males, and is worthy of further attention.

ACKNOWLEDGEMENTS

We thank P.D. Dang for field assistance, and S. Zschokke for use of his photograph of a web of *N. senegalensis*. Comments from D. J. Irschick, A. Herrel, and an anonymous referee greatly improved this paper. This research was supported by Sigma-Xi grants-in-aid to both authors.

REFERENCES

Anderson JF. 1974. Responses to starvation in the spiders *Lycosa lenta* (Hentz) and *Filistata hibernalis* (Hentz). *Ecology* **55:** 576–585.

Andersson M. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.

Andrade MCB. 1998. Female hunger can explain variation in cannibalistic behavior despite male sacrifice in redback spiders. *Behavioral Ecology* **9:** 33–42.

Arnold SJ. 1983. Morphology, performance, and fitness. *American Zoologist* **23:** 347–361.

Arnqvist G, Nilsson T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour* **60:** 145–164.

Blackledge TA, Coddington JA, Gillespie RG. 2003. Are three-dimensional spider webs defensive adaptations? *Ecology Letters* **6:** 13–18.

Brown KM. 1981. Foraging ecology and niche partitioning in orb-weaving spiders. *Oecologia* **50:** 380–385.

Chapman T, Arnqvist G, Bangham J, Rowe L. 2003. Sexual conflict. *Trends in Ecology and Evolution* **18:** 41–47.

Christenson TE, Brown SG, Wenzl PA, Hill EM, Goist KC. 1985. Mating behavior of the golden-orb-weaving spider, *Nephila clavipes* 1: Female receptivity and male courtship. *Journal of Comparative Psychology* **99:** 160–166.

Craig CL. 1986. Orb web visibility: the influence of insect flight behavior and visual physiology on the evolution of web designs in the Araenoidea. *Animal Behavior* **34:** 54–68.

Craig CL. 1987. The significance of spider size to the diversification of spider web architectures and spider reproductive modes. *American Naturalist* **129:** 47–68.

Craig CL. 2003. *Spiderwebs and silk: Tracing evolution from molecules, to genes, to phenotypes*. Oxford: Oxford University Press.

Danielson-Francois A, Fetterer CA, Smallwood PD. 2002. Body condition and mate choice in *Tetragnatha elongata* (Araneae, Tetragnathidae). *Journal of Arachnology* **30:** 20–30.

Eberhard WG. 1971. The ecology of the web of *Uloborus diversus*. *Oecologia* **8:** 328–342.

Eberhard WG. 1989. Effects of web orientation and spider size on prey retention. *Bulletin of the British Arachnological Society* **8:** 45–48.

Eberhard WG. 1990. Function and phylogeny of spider webs. *Annual review of Ecology and Systematics* **21:** 341–372.

Elgar MA. 1991. Sexual cannibalism, size dimorphism and courtship behavior in orb-weaving spiders (Araneae). *Evolution* **45:** 444–448.

Fedorka KM, Mousseau TA. 2002. Material and genetic benefits of female multiple mating and polyandry. *Animal Behaviour* **64:** 361–367.

Foelix RF. 1996. *Biology of spiders*. Oxford: Oxford University Press.

Foerster K, Delhay K, Johnsen A, Lifjeld JT, Kempenaers B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature* **425:** 714–717.

Frontier S. 1976. Etude de la decroissance des valeurs propres dans un analyse en composantes principales: comparison avec le model de baton brise. *Journal of Experimental Marine Biology and Ecology* **25:** 67–75.

Head G. 1995. Selection on size and fecundity and variation in the degree of sexual size dimorphism among spider species. *Evolution* **49:** 776–782.

Herberstein ME, Schneider JM, Elgar MA. 2002. Costs of courtship and mating in a sexually cannibalistic orb-web spider: female mating strategies and their consequences for males. *Behavioral Ecology and Sociobiology* **51:** 440–446.

Herrel A, Meyers JJ, Vanhooydonck B. 2001. Relations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*). *Biological Journal of the Linnean Society* **74:** 305–314.

Higgins LE. 1990. Variation in foraging investment during the intermolt interval and before egg-laying in the spider *Nephila clavipes* (Araneae: Araneidae). *Journal of Insect Behavior* **3:** 773–783.

Hormiga G, Scharff N, Coddington JA. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Obiculariae). *Systematic. Biology* **49:** 435–462.

Hosken DJ, Garner TWJ, Tregenza T, Wedell N, Ward PI. 2003. Superior sperm competitors sire higher-quality young. *Proceedings of the Royal SocietyB* **270:** 1933–1938.

Irschick DJ, Garland T Jr. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annual. Reviews in Ecology and Systematics* **32:** 367–396.

Irschick DJ, Losos JB. 1998. A comparative analysis of the ecological significance of locomotor performance in Caribbean *Anolis* lizards. *Evolution* **52:** 319–226.

Jackson DA. 1993. Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. *Ecology* **74:** 2204–2214.

Jennions MD, Petrie M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews* **75:** 21–64.

Johnstone RA, Keller L. 2000. How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. *American Naturalist* **156:** 368–377.

Kachigan SK. 1991. *Multivariate statistical analysis: a conceptual introduction*. New York: Radius Press.

Langerhans RB, Layman CA, Langerhans AK, Dewitt TJ. 2003. Habitat-associated morphological divergence in two Neotropical fish species. *Biological Journal of the Linnean Society* **80:** 689–698.

Liersch S, Schmidt-Hempel P. 1998. Genetic variation between social insect colonies reduces parasite load. *Proceedings of the Royal Society of London B* **265:** 221–225.

Losos JB. 1990. The evolution of form and function: morphology and locomotor performance ability in West Indian *Anolis* lizards. *Evolution* **44:** 1189–1203.

Marshall SD, Gittleman JL. 1994. Clutch size in spiders: is more better? *Functional Ecology* **8:** 118–124.

Moore CW. 1977. Life-cycle, habitat, and variation in selected web parameters in a spider, *Nephila clavipes* Koch (Araneidae). *American Midland Naturalist* **98:** 95–108.

Newman JA, Elgar MA. 1991. Sexual cannibalism in orb-weaving spiders: an economic model. *American Naturalist* **138:** 1372–1395.

Nosil P, Crespi BJ. 2004. Does gene flow constrain adaptive divergence or vice versa? A test using ecomorphology and sexual isolation in *Timema cristinae* walking sticks. *Evolution* **58:** 102–112.

Olive CW. 1982. Behavioral response of a sit-and-wait predator to spatial variation in foraging gain. *Ecology* **63:** 912–929.

Prenter J, Elwood RW, Montgomery WI. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. *Evolution* **53:** 1987–1994.

Prenter J, Elwood RW, Montgomery WI. 2003. Mate-guarding, competition, and variation in size in male orb-web spiders, *Metellina segmentata*: a field experiment. *Animal Behaviour* **66:** 1053–1058.

Schneider JM, Elgar MA. 2001. Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives. *Behavioral Ecology and Sociobiology* **12:** 547–552.

Sherman PM. 1994. The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Animal Behaviour* **48:** 19–34.

Simmons LW. 2003. The evolution of polyandry: patterns of genotypic variation in female mating frequency, male fertilization success and a test of the sexy-sperm hypothesis. *Journal of Evolutionary Biology* **16:** 624–634.

Sokal RR, Rohlf FJ. 1981. *Biometry*. New York: WH Freeman.

Suter RB. 1978. *Cyclosa turbinata* (Araneae: Araneidae): prey discrimination via web-borne vibrations. *Behavioral Ecology and Sociobiology* **3:** 283–296.

Taylor PW, Hasson O, Clark DL. 1999. Body postures and patterns as amplifiers of physical condition. *Proceedings of the Royal Society of London B* **267:** 917–922.

Uetz GW. 1992. Foraging strategies of spiders. *Trends in Ecology and Evolution* **7:** 155–158.

Vahed K. 1998. The function of nuptial feeding in insects: a review of empirical studies. *Biological Reviews* **73:** 43–78.

Venner S, Bel-Venner M, Pasquet A, Leborgne R. 2002. Body-mass-dependent cost of web-building behavior in an orb weaving spider, *Zigiella x-notata*. *Naturwissenshaften* **90:** 269–272.

Vincent SE, Herrel A, Irschick DJ. 2004. Ontogeny of intersexual head shape and prey selection in the pitviper *Agkistrodon piscivorus*. *Biological Journal of the Linnean Society* **81:** 151–159.

Vollrath F. 1987. Foraging, growth, and reproductive success. In: Nentwig W, ed. *Ecophysiology of spiders.* Berlin: Springer, 357–370.

Wainwright PC, Bellwood DR, Westneat MW. 2002. Ecomorphology of locomotion in labrid fishes. *Environmental Biology of Fishes* **65:** 47–62.

Wainwright PC, Reilly SM. 1994. *Ecological morphology: integrative organismal biology*. Chicago, IL: University of Chicago Press.

Zschokke S. 1997. Factors influencing the size of the orb web in *Araneus diadematus*. *Proceedings of the 16th European Colloquium of Arachnology, Zabka, M.Wyzsza Szkola Rolniczo-Pedagogiczna, Siedlce (Poland)* 329–334.