2008. The Journal of Arachnology 36:210–212

SHORT COMMUNICATION

The costs of male courtship and potential benefits of male choice for large mates in *Phidippus clarus* (Araneae, Salticidae)

Chad D. Hoefler[1]: Organismic and Evolutionary Biology, Department of Plant, Soil, and Insect Sciences, University of Massachusetts, Amherst, Massachusetts 01003, USA

Abstract. Despite a wealth of research on the benefits of mate choice, empirical evidence for the costs of courtship is scarce. Understanding the interplay between the costs and benefits of reproductive behaviors is critical to our understanding of sexual selection. I present a study designed to explore the potential reproductive benefits of male choosiness for large mates as well as the costs of courtship in the jumping spider *Phidippus clarus* (Keyserling 1885). My findings suggest that a positive relationship between female tibia length and the number of emerging spiderlings may underlie male choice for large females. However, this benefit may be mitigated by the longevity costs of courtship. Further investigation of the potential trade-offs between the benefits of male preferences for large females and the costs of courtship in this species is required.

Keywords: Sexual selection, survivorship, fitness, jumping spider

The costs and benefits of courtship and mate choice are of critical importance to our understanding of sexual selection, and it has been widely accepted that sexual traits associated with courtship increase fitness. However, currently favored viability indicator (good genes) and Fisherian self-reinforcing models of sexual selection require that courtship behaviors and associated morphological traits have evolutionary costs that balance their benefit (Fisher 1958; Zahavi 1975; Kirkpatrick 1982; Andersson 1986). Although significant research effort has been directed towards the fitness benefits that individuals derive from courtship and mate choice (Petrie 1992; Johnstone 1995; Rypstra et al. 2003), quantification of costs has been rare (Kotiaho 2001).

I report an investigation designed to explore some of the fitness costs of male courtship and mating as well as the potential benefits of male choice for large mates in the jumping spider *Phidippus clarus* (Keyserling 1885). *P. clarus* is a widespread, sexually dimorphic jumping spider that inhabits old fields throughout North America. Adult females build silken nests that are used when mating, ovipositing, and guarding young (Hoefler & Jakob 2006). In Massachusetts as well as other parts of the USA (e.g., Roach 1988), *P. clarus* has a relatively restricted reproductive cycle compared to other congeners mating in early to mid July and ovipositing in August (pers. obs.). Hoefler (2007) discovered that cohabiting pairs (= adult male guarding penultimate instar female) of *P. clarus* were size-assortatively matched for tibia length (front legs). Adult males are choosy: in outdoor simultaneous choice tests, small and large adult males preferentially courted and cohabited with females that had longer tibias, a trait that was inversely correlated with female maturation. Further, adult males demonstrated preferences for large adult females (that mature early) when only female silk and associated cues were present (Hoefler 2007). This might suggest that males discriminate between females on the basis of pheromones or other cues associated with silk, which indicate closeness to maturity as well as overall body size. However, because female tibia length appeared to be important for male discrimination (and highly correlated with other traits potentially used for discrimination) (Hoefler 2007), my specific aims in the current study were to (1) explore the potential benefits of male preferences for large females by examining the relationship between maternal tibia length and the number of offspring that emerged from egg sacs and to (2) investigate the potential costs of male courtship and mating by quantifying the effect that these behaviors had on the survivorship of males. Voucher specimens were deposited in the University of Massachusetts, Amherst insect collection.

P. clarus readily use artificial nest tubes in the field to build silken retreats, which are important sites for reproduction among other things (Hoefler & Jakob 2006). During the first two weeks of June 2003, I haphazardly placed 90 cm tall surveyors flags (Ben Meadows, Janesville, Wisconsin, USA) made of wire poles with 7.5 × 6.5 cm plastic flags in old fields in Amherst (42.3736°N, 72.5208°W) and Hadley (42.3606°N, 72.5714°W), Massachusetts, USA. I made artificial nest tubes (3.8 cm long, 1.5 cm diameter) of plastic plumber's tubing, painted them black with spray paint (Krylon flat black, Sherwin-Williams, Cleveland, Ohio, USA), and tied them to the wire pole of surveyor flags such that they were positioned horizontally. I returned to the fields in mid September 2003 and collected nest tubes with egg sacs and guarding adult females and maintained them in the laboratory individually in plastic cages (18 cm × 13 cm × 11 cm) on a 13:11 h L:D cycle at approximately 26° C until spiderlings emerged. I offered females approximately five early-instar crickets (*Acheta domestica*, Top Hat Cricket Farm, Kalamazoo, Michigan, USA) per week, and provided water ad libitum in test tubes plugged with cotton. I recorded the right front tibia length of each adult female using dial calipers under a dissecting microscope and measured them to the nearest 0.01 mm. Adult females were immobilized briefly with carbon dioxide gas before measurements were recorded. As spiderlings emerged, they were separated into individual Petri dishes (3.5 cm diameter, 1 cm high) to minimize potential counting error. Petri dishes were labeled according to identification numbers assigned to mothers. After all spiderlings emerged, I regressed female tibia length against the number of hatched spiderlings and discovered that tibia length significantly predicted the number of spiderlings ($F_{1,35} = 156.23$, $n = 37$, $r^2 = .817$, $P < 0.0001$, Fig. 1).

Concurrently, I examined the effects of male courtship and mating on male longevity. In early June 2003, I collected 47 penultimate males (= instar not associated with females), raised them to adulthood in the laboratory as described above, and recorded the

---

[1] Current address: Center for Animal Behavior, Department of Zoology, Miami University, Oxford, Ohio 45056, USA. E-mail: hoeflecd@muohio.edu.

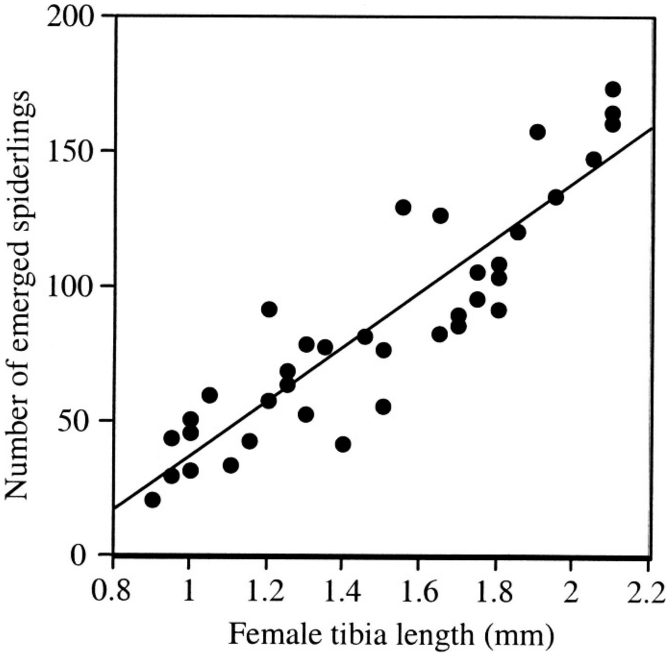

Figure 1.—The number of emerged *P. clarus* spiderlings regressed against the length of the mother's tibia.

date of their final molt. Antepenultimate females (n = 227) were also collected and maintained as previously described through their penultimate and adult instars. Construction paper blinders were placed between cages housing males to prevent them from seeing each other; all male cages were placed away from female cages in the laboratory.

After all males matured, I randomly divided them into two treatment groups and one control group: courtship experience (n = 16), courtship and mating experience (n = 17), and naïve (n = 14). In early July 2003, individual males assigned to the courtship experience treatment were placed in the cage of a randomly selected penultimate female for 1 h daily over a period of 5 consecutive days. Males were placed with a different, randomly selected female each day. All males courted penultimate females by vigorously waving their front legs and abdomens while moving from one side of the cage to the other. On day 6, males were placed into empty cages for 1 h. After trials, males were returned to their cages, where they were offered up to 5 crickets (depending upon how many were currently in the male's cage). I followed this same protocol for males assigned to the courtship and mating experience treatment; however, on day 6, males were placed in a randomly selected cage housing an adult female, and the pair was allowed to mate. All males attempted to insert their pedipalps into the female's epigynum, but I did not determine whether sperm were transferred. Males assigned to the naïve group were placed in different empty cages for 1 hour a day over a period of 6 consecutive days (crickets were offered as described above). Following the 6-day treatment period, males were maintained in the laboratory as described above until they died. Date of death was recorded for all males. I compared the survival distributions (date of final molt to date of death) using Kaplan-Meier survival analysis (Kaplan & Meier 1958). I used the non-parametric Kaplan-Meier product limit estimator to test for a significant treatment effect on the median survival distribution. Additional pairwise comparisons were made via the logrank (Mantel-Cox) test.

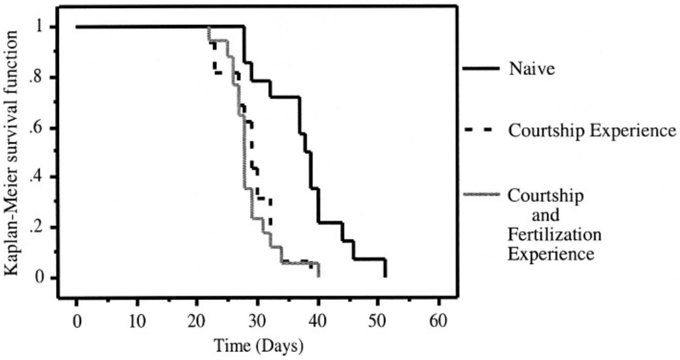

Figure 2.—Survival distributions of adult *P. clarus* males from naïve, courtship experience, and courtship and mating experience groups as a function of the number of days after their final molt.

Male courtship and mating had a significant effect on the longevity of males (Mantel-Cox logrank test: χ^2= 16.48, n = 47, P = 0.0003, Fig. 2). Males assigned to the naïve treatment lived significantly longer than males assigned to the courtship experience treatment (P = 0.0002) as well as males assigned to the courtship and mating experience treatment ($P < 0.0001$). Male longevity did not differ between the courtship experience treatment and courtship and mating experience treatment (P = 0.972).

Results from my study are consistent with the widely accepted paradigm that male arthropods can maximize fitness by mating with large females. This may explain male choice in *P. clarus* (Hoefler 2007): if a male is unable to mate with all reproductive females in a population, he should benefit by selecting females capable of producing more offspring. Male mate choice decisions would be expected to be based on female features that are correlated with potential reproductive success, such as body size (Gwynne 1991; Owens & Thompson 1994; Altmann 1997). However, costs incurred during courtship may mitigate the benefit.

In the current study, I discovered that adult female tibia length significantly predicted the number of spiderlings that emerged from egg sacs. This finding is consistent with and may underlie Hoefler's (2007) discovery that male *P. clarus* prefer females with long tibias. Generally, clutch size increases with female body size in many arthropods, including spiders (Marshall & Gittleman 1994; Simpson 1995; Jann & Ward 1999; Fox & Czesak 2000; Skow & Jakob 2003). For example, tibia-patella length was highly correlated with egg clutch size in the pholcid spider *Holocnemus pluchei* (Scopoli 1763) (Skow & Jakob 2003). This common pattern in arthropods may implicate male choice as something that may be more widespread than presently apparent (Bonduriansky 2001).

Combined with previous studies of mating behaviors in *P. clarus*, the advantage of male choice for large females would appear to be twofold: (1) female size and number of progeny are positively correlated, and (2) larger females mature before smaller females creating opportunities for polygynous mating (Hoefler 2007). It is important to acknowledge that I did not monitor female mating behavior in the field. Therefore, I am unaware if females mated multiply and if polyandry affects the number of eggs produced, as has been found in other arthropods (Moya-Larano & Fox 2006). Evidence from other salticids suggests that these spiders do sometimes mate again, but are much less prone to mating after their first copulation (Jackson 1981).

I discovered that courting (and mating) male *P. clarus* had significantly reduced survivorship than males who had no experience with females. This may have been a consequence of the energetic costs of courtship. Interestingly, in between trials with females, males were maintained individually in cages with cricket prey available. Although I did not quantify prey consumption, males appeared to feed very rarely. Thus, they may not have been able to recoup the loss of energy spent on courtship.

A trade-off between the fitness benefit of courting, discriminating between females, mating with large females, and the reduced lifespan associated with courtship may play a vital role in male reproductive success. Reproductive behaviors have been shown to reduce lifespan in other species. For instance, courtship significantly decreases longevity in male vinegar flies (Cordts & Partridge 1996), tsetse flies (Clutton-Brock & Langley 1997), and the drumming wolf spider *Hygrolycosa rubrofasciata* (Ohlert 1865) (Kotiaho 2000). However, it is currently unknown if male courtship is integral to male discrimination. If courtship is evolutionarily costly and discrimination can be achieved without courtship, it would be advantageous for males to avoid courtship with unprofitable potential mates. Interestingly all males in the courtship treatment and courtship and fertilization treatment courted all females, which varied in size. Although only one female was present with a male at a given time, it would appear that male courtship is very common when females are present.

In addition to energetic costs, male *P. clarus* courtship may have other costs. Predators and parasitoids often exploit the sexual displays of their prey in order to locate them (Cade 1975; Wagner 1996; Zuk et al. 1998). Pompilid wasps have been observed attacking and subduing *P. clarus* in the field (Hoefler, pers. obs.); courting males may be more susceptible than females due to their overt courtship displays and because they often guard females outside of the silken retreat where they are exposed. Socially imposed costs, which may take the form of increased male aggression towards displaying males (Borgia 1995; Candolin 1997; Kotiaho 2001), may also reduce male fitness via energetic costs and/or injury.

To ascertain with greater certainty the value of spider males mating with larger females, researchers conducting future studies should consider experimental control over female mating opportunity as well as measures of fitness other than offspring number. Similarly, future studies of how reduced lifespan from courtship affects lifetime reproductive success will improve our understanding of the trade-off between sexual behaviors and their underlying costs.

This research was based upon work supported by the Cooperative State Research Extension, Education Service, U.S. Department of Agriculture, Massachusetts Agricultural Experiment Station, under Project No. MAS 00829 and an American Arachnological Society student grant. Additional support came from a National Science Foundation Short-term Grant for Exploratory Research and a University of Massachusetts Faculty Research Grant. I thank Elizabeth Jakob, Ben Normark, Jeff Podos, Ron Prokopy, and Paul Sievert for their comments and suggestions. Lastly, I would like to thank Robert Jackson, Gail Stratton, and an anonymous reviewer for critical and helpful remarks on an earlier draft of this manuscript.

LITERATURE CITED

Altmann, J. 1997. Mate choice and intrasexual reproductive competition: contributions to reproduction that go beyond acquiring more mates. Pp. 320–333. *In* Feminism and Evolutionary Biology. (P.A. Gowaty, ed.). Chapman & Hall, New York.

Andersson, M. 1986. Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. Evolution 40:804–816.

Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. Biological Reviews 76:305–339.

Borgia, G. 1995. Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhyncus violaceus*). Behavioral Ecology and Sociobiology 18:91–100.

Cade, W.H. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. Science 190:1312–1313.

Candolin, U. 1997. Predation risk affects courtship and attractiveness of competing threespine stickleback males. Behavioral Ecology and Sociobiology 41:81–87.

Clutton-Brock, T. & P. Langley. 1997. Persistent courtship reduces male and female longevity in captive tsetse flies *Glossina morsitans morsitans* Westwood (Diptera: Glossinidae). Behavioral Ecology 8:392–395.

Cordts, R. & L. Partridge. 1996. Courtship reduces longevity of male *Drosophila melanogaster*. Animal Behaviour 52:269–278.

Fisher, R.A. 1958. The Genetical Theory of Natural Selection. Second edition. Oxford University Press, New York. 291 pp.

Fox, C.W. & M.E. Czesak. 2000. Evolutionary ecology of progeny size in arthropods. Annual Review of Entomology 45:341–369.

Gwynne, D.T. 1991. Sexual competition among females: what causes courtship-role reversal? Trends in Ecology & Evolution 6:118–121.

Hoefler, C.D. 2007. Male mate choice and size-assortative pairing in a jumping spider. Animal Behaviour 73:943–954.

Hoefler, C.D. & E.M. Jakob. 2006. Jumping spiders in space: movement patterns, nest site fidelity, and the use of beacons. Animal Behaviour 71:109–116.

Jackson, R.R. 1981. Relationship between reproductive security and intersexual selection in a jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). Evolution 35:601–604.

Jann, P. & P.I. Ward. 1999. Maternal effects and their consequences for offspring fitness in the Yellow Dung Fly. Functional Ecology 13:51–58.

Johnstone, R.A. 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. Biological Reviews 70:1–65.

Kaplan, E.L. & P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. Evolution 36:1–12.

Kotiaho, J.S. 2000. Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. Behavioral Ecology and Sociobiology 48:188–194.

Kotiaho, J.S. 2001. Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. Biological Reviews 76:365–376.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? Functional Ecology 8:118–124.

Moya-Larano, J. & C.W. Fox. 2006. Ejaculate size, second male size, and moderate polyandry increase female fecundity in a seed beetle. Behavioral Ecology 17:940–946.

Owens, I.P.F. & D.B.A. Thompson. 1994. Sex differences, sex ratios, and sex roles. Proceedings of the Royal Society of London, Series B 258:93–99.

Petrie, M. 1992. Peacocks with low mating success are more likely to suffer predation. Animal Behaviour 44:585–596.

Roach, S.H. 1988. Reproductive periods of *Phidippus* species (Araneae, Salticidae) in South Carolina. Journal of Arachnology 16:95–101.

Rypstra, A.L., C. Weig, S.E. Walker & M.H. Persons. 2003. Mutual mate assessment in wolf spiders: differences in the cues used by males and females. Ethology 109:315–325.

Simpson, M.R. 1995. Covariation of spider egg and clutch size: the influence of foraging and parental care. Ecology 76:795–800.

Skow, C.D. & E.M. Jakob. 2003. Effects of maternal body size on clutch size and egg weight in a pholcid spider (*Holocnemus pluchei*). Journal of Arachnology 31:305–308.

Wagner, W.E.J. 1996. Convergent song preferences between female field crickets and acoustically oriented parasitoid flies. Behavioral Ecology 7:279–285.

Zahavi, A. 1975. Mate selection—a selection for a handicap. Journal of Theoretical Biology 53:205–214.

Zuk, M., J.R. Rotenberry & L.W. Simmons. 1998. Calling songs of field crickets (*Teleogryllus oceanicus*) with and without phonotactic parasitoid infection. Evolution 52:166–171.

Manuscript received 2 February 2007, revised 7 September 2007.