

## Contrasting energetic costs of courtship signaling in two wolf spiders having divergent courtship behaviors

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**Abstract.** Energetic costs of courtship behavior were measured for two sympatric wolf spiders that are reproductively isolated based on distinct male courtship behaviors with different signaling modes and activity levels: *Schizocosa ocreata* (Hentz 1844) uses multi-modal communication (visual and seismic signals) and an actively-moving courtship display, whereas *S. rovneri* (Uetz & Dondale 1979) uses only seismic signals produced while stationary. To test for increased energetic expense of more complex multimodal courtship in *S. ocreata*, we recorded peak CO<sub>2</sub> output for male spiders standing, walking, or courting. We found that peak CO<sub>2</sub> output while standing or walking was similar between species. Courtship behavior of *S. ocreata* produced greater peak CO<sub>2</sub> output than these other behaviors, and was significantly greater than peak CO<sub>2</sub> output of *S. rovneri* courtship, which was not different from that of locomotion. Hence, unequal energy expenditure related to the modality of the males' courtship displays resulted in different energetic costs for courting male spiders. Male courtship vigor may serve as a criterion for female mate choice in *Schizocosa*.

**Keywords:** Courtship, energetics, *Schizocosa*, respiration, sexual selection

### INTRODUCTION

Differences in male courtship displays between spider species may serve as behavioral isolating mechanisms for closely-related taxa (Stratton & Uetz 1981, 1986; Miller et al. 1998; Stratton 2005), but may also reflect the influence of sexual selection based in part on differential energetic costs (Kotiaho et al. 1998; Parri et al. 2002; Delaney et al. 2007; Byers et al. 2010). Much support for “handicap” or “good genes” models of sexual selection suggests that females prefer males capable of sustaining higher levels of energetically costly motor performance (see review by Byers et al. 2010), because active, complex courtship display behaviors provide “honest” information to females about male condition or quality (e.g., Zahavi 1975; Zuk 1991; Andersson 1994; Kotiaho et al. 1996, 1998). For example, in the well-studied European wolf spider *Hygrolycosa rubrofasciata* (Ohlert 1865), females choose males on the basis of drumming rates, which are good predictors of male condition and viability (Kotiaho et al. 1996; Kotiaho et al. 1998; Kotiaho 2000; Ahtianen et al. 2005, 2006).

Wolf spiders (Lycosidae) use active courtship displays and multimodal communication (visual and seismic cues) to varying degrees (Kotiaho et al. 1998; Hebets & Uetz 1999; Hebets et al. 2006; Uetz & Roberts 2002; Uetz et al. 2009). Within the genus *Schizocosa*, the *S. ocreata* clade contains 6–8 species that apparently have arisen via behavioral isolation driven by sexual selection (Miller et al. 1998; Stratton 2005). Members of this clade are similar in size and coloration, have nearly identical genitalia, and females are largely indistinguishable. Males, however, vary in the degree of decoration of their forelegs (ranging from little or no pigmentation to dark pigment and tufts of bristles) and courtship behavior (stationary vs. active movement; unimodal vs. multimodal signals) (Stratton & Uetz 1981, 1986; Hebets & Uetz 2000; Uetz & Roberts 2002; Stratton 2005). While energetic costs of courtship signaling are currently unknown for *Schizocosa*,

several studies suggest that highly active multimodal signaling may be more costly (Delaney et al. 2007; Roberts et al. 2007; Uetz et al. 2009). In this study, we test this hypothesis by examining the energetic costs of courtship display for two well-studied sibling species: *Schizocosa ocreata* (Hentz 1844) and *S. rovneri* (Uetz & Dondale 1979). Given the observed active, multimodal courtship of *S. ocreata* versus the more stationary, unimodal courtship of *S. rovneri* (Delaney et al. 2007; Uetz et al. 2009), we predicted that *S. ocreata* will incur higher energetic costs than its sibling species.

### METHODS

**Study species.**—The brush-legged wolf spider, *Schizocosa ocreata*, and its sympatric sibling species, *S. rovneri* are often referred to as “ethospecies”, because while physically capable of interbreeding (Stratton & Uetz 1986), the species remain isolated due to distinct communication behaviors permitting pre-mating species recognition and reproductive isolation (Stratton & Uetz 1981, 1986). Male *S. ocreata* possess dark pigmentation and conspicuous tufts of bristles on the forelegs used in visual courtship displays while these tufts and visual displays are lacking in *S. rovneri*. Males court conspecific and heterospecific females and their silk with equal frequency (Roberts & Uetz 2004), but females only mate with conspecifics (Uetz & Denterlein 1979; Stratton & Uetz 1981). Despite the highly effective behavioral barrier, these species are highly similar at the molecular phylogenetic level (Hebets & Vink 2007), potentially interfertile, and capable of producing interspecific hybrids (Stratton & Uetz 1981, 1986; Orr & Uetz unpubl.), suggesting a relatively recent evolutionary divergence (Stratton 2005).

Courtship display behaviors differ considerably between these two species (Delaney et al. 2007; Uetz et al. 2009). The courtship of male *S. rovneri* consists predominately of a single display performed while stationary. The body “bounce” combines substratum-coupled stridulation (rotation of pedipalps) and percussion (the body, abdomen and/or chelicerae

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sometimes strike the substratum). A “leg extend” display is also occasionally produced. In contrast, the courtship display of *S. ocreata* is far more active, and consists of two displays performed during locomotion (“double tap” and “jerky tap”) and two while stationary (“leg extend” and “wave/arch”). Seismic signals from stridulation (pedipalps) and percussion (abdomen and chelicerae striking the substratum) are produced simultaneously with visual signals during the “jerky tap” display. Analyses here were centered around three main behaviors: stationary (the spiders remains motionless), locomotion (the spider walks, explores, or otherwise moves around), and courtship (specific courtship behaviors displayed as described above).

**Animal maintenance.**—We collected immature spiders in April–May 1997 from sites containing only one of the two species: *S. ocreata* from the Rowe Woods facility of the Cincinnati Nature Center, Clermont Co., Ohio, and *S. rovneri* from Sandy Run Creek, Boone Co., Kentucky. We maintained all spiders individually in the laboratory until sexual maturity in opaque plastic containers (10 cm diam.) under identical controlled conditions (22–24° C; light:dark cycle = 13:11 h). All spiders received water ad libitum and 4–5, 10-day old live crickets (*Acheta domestica*) as food once/week.

**Measurement of energetic output.**—We collected data on CO<sub>2</sub>-production as a function of male behavior using a Sable Systems TR-2 flow-through respirometry system. A multiplexer controlled flow of CO<sub>2</sub>-free air (75 ml/min) and gas mixtures throughout the purging and data collection segments of each trial. We monitored temperature continuously throughout test runs using integrated thermocouples. Data acquisition, integration, and initial analyses used Sable Systems software (Sable Systems, Salt Lake City, Utah). Data were acquired from the test chambers and data logger at one-second intervals.

We first placed each of 13 male *Schizocosa* spiders into a 25 ml, cylindrical, clear acrylic test chamber with stoppers fitted with tube couplings and valves at each end. The animal acclimated at least 10 min in the chamber while chamber temperature stabilized. Immediately before testing, we purged the chamber to create a standard air environment of 15-ppm CO<sub>2</sub>. After purging and standardization, we attached the chamber to the respirometer and the trial began.

Each 20 min trial consisted of sequentially logging non-courtship behavior followed by courtship using two 10-min periods of collecting, observing, and logging behaviors displayed by an individual spider using the integrated behavior logging feature of the software. The first 10 min provided baseline measurements of CO<sub>2</sub> liberation during stationary and locomotory behaviors. After the initial 10 min, we introduced a piece of paper (~1 × 3 cm) cut from the substrate (“cage card”) of a female conspecific *Schizocosa* into the test chamber with the male. This paper held chemical cues triggering courtship in the male (Roberts & Uetz 2004 a,b; Roberts & Uetz 2005). We purged the chamber and again placed the spider into the respirometer for 10 min to monitor and log courtship behaviors as above.

We adjusted measurements of liberated carbon dioxide relative to spider mass, temperature, and observed duration of behaviors via the Sable software and graphed the results (Fig. 1). We extracted values for observed peaks of CO<sub>2</sub>

output, (μl/g/h) during selected periods of three main behaviors: stationary, locomotion, and courtship, which then served as the bases for analyses. We determined the peaks associated with these behaviors by visually inspecting the respirometer output of lagged synchrony with time-stamped event recording (see Fig. 1).

We recorded multiple peak CO<sub>2</sub> values for each behavioral category for seven *S. ocreata* and six *S. rovneri* males (Leger & Didrichsons 1994), and analyzed for interspecific differences in peak values using the Mann-Whitney U-test. We also calculated means ± SEM for each of the six data categories in order to calculate the ratios of energetic output.

## RESULTS

During the first observation period, all males ( $n = 13$ ) alternated bouts of locomotor activity with periods of stationary resting behavior (Fig. 1). They all exhibited courtship behavior during the second observation period (after purging the chamber) upon contacting the paper substrate containing silk from conspecific females.

As expected, locomoting spiders produced much higher peak CO<sub>2</sub> output relative to stationary ones: *S. rovneri* = 120.6%; *S. ocreata* = 107.7% (Fig. 2). Furthermore, courting males were even more active than when they were at rest: *S. rovneri* = 153.2%; *S. ocreata* = 225.4% (Fig. 2).

Analyses of peak CO<sub>2</sub> output revealed no differences between species for stationary or locomotor behaviors (Fig. 2). In contrast, courting *S. ocreata* males had a significantly greater peak CO<sub>2</sub> output than *S. rovneri* males ( $U = 560$ ,  $P = 0.022$ ; Fig. 2). The more active courtship of *S. ocreata*, comprised of a “jerky-tap” display which includes forward locomotion, leg-tapping, and leg-waving, produced a 36.6% higher level of peak CO<sub>2</sub> output than *S. rovneri*. Additionally, the degree of difference between levels of peak CO<sub>2</sub> output during courtship and locomotor activity for *S. ocreata* was much greater (56.6%) than that for *S. rovneri* (14.7%), who remain stationary during courtship. Thus, the rate of increase for energetic costs for the behavioral transition from a stationary state to active courtship is greater for *S. ocreata* than *S. rovneri*.

## DISCUSSION

Our results show that, while stationary and resting metabolism of both spider species are similar, courtship is more energetically expensive for *Schizocosa ocreata* than it is for *S. rovneri* males. The multi-modal signaling of *S. ocreata* (with visual and seismic components) likely accounts for a greater difference in resting versus courtship CO<sub>2</sub> liberation compared to that of the stationary unimodal display of *S. rovneri* (seismic only). Hence, differences in CO<sub>2</sub> output during courtship between these species supports our initial hypothesis.

Using peak CO<sub>2</sub> values as a metric of energetic output by spiders is complicated because a proportion of the expired CO<sub>2</sub> could originate from hemolymph bicarbonate due to lactate production (Prestwich 1983, 1988a,b). Lactate reaches maximum concentration approximately 10 min after vigorous exercise in theraphosid spiders (i.e. tarantulas on treadmills, Paul & Storz 1987). In lycosids, depending on intensity of activity, lactate may reach very high levels in 30 s, or it may

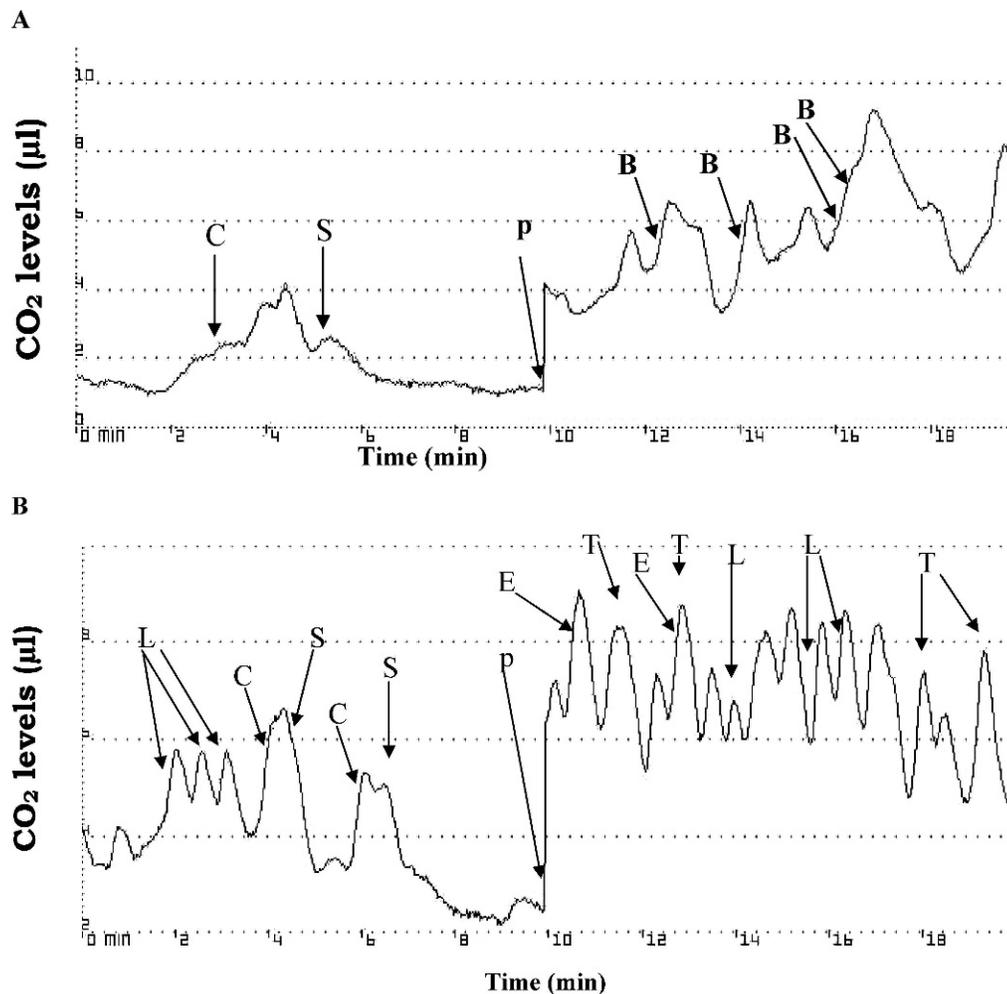


Figure 1.—Representative CO<sub>2</sub> output profiles for male *Schizocosa* during the two observation periods (first period = 10 min resting/walking; second period = 10 min active courtship after stimulation of chemical cues from silk of conspecific female): **A.** Male *S. rovneri*; **B.** Male *S. ocreata*. Bouts of different behavioral activities are indicated by arrows on the graph (note different ordinate scales for A and B). Abbreviations: B = bounce (the spider strikes the substrate with the sternum); C = climb (moving up the chamber's side and supporting the body on rear legs); E = explore (using forelegs to probe the area ahead or below the spider); L = locomotion (walking or generally moving around the chamber); p = purge test chamber after addition of female silk; S = stridulate (the spider places tips of palpal tarsus on substrate and flexes stridulatory organ between palpal tibia and tarsus); T = tap (simultaneous raising of forelegs prior to simultaneously striking the substrate with both legs).

not accumulate significantly even after longer activities (Prestwich pers. comm). Thus, the influence of lactate on VDCO<sub>2</sub> (= the volume of CO<sub>2</sub> produced per unit time) may complicate the comparison of different activities in dissimilar species.

Our study compares very similar species performing similar types of activities. Our analyses used VDCO<sub>2</sub> recorded only at peaks of activity for the three basic behaviors, and possibly overestimates aerobic metabolism during these activities. However, because we compared very similar behaviors in sibling species, overestimates are likely to be parallel, and useful comparisons are still possible. In fact, the potential overestimate of aerobic metabolism obtained by using VDCO<sub>2</sub> in these specific cases is advantageous because it qualitatively accounts for any anaerobic metabolism contributing to the total cost of the activity (Prestwich pers. comm.). Measurements of VDO<sub>2</sub> alone would not do this. Thus, in these limited

comparisons, VDCO<sub>2</sub> should represent a reasonable metric of comparison.

There are two non-exclusive hypotheses that might explain observed differences in the energetic expense of courtship behavior between these species. For example, differences may reflect the influence of environmental constraints on signaling. Attenuation of seismic courtship signals in leaf litter microhabitats has been suggested as the reason *S. ocreata* uses multi-modal signaling incorporating simultaneous visual signals (active leg-waving and tapping) along with production of seismic signals by stridulation and percussion (Scheffer et al. 1996; Uetz 2000; Uetz & Roberts 2002; Uetz et al. 2009). In addition, multiple substratum types (leaves, bark, twigs, soil, rocks) within the complex litter habitat vary in capacity to convey seismic signals (Elias et al. 2004; Hebets et al. 2008; Elias et al. 2010; Gordon & Uetz, in review). Thus, *S. ocreata* courtship displays must include more overt visual components

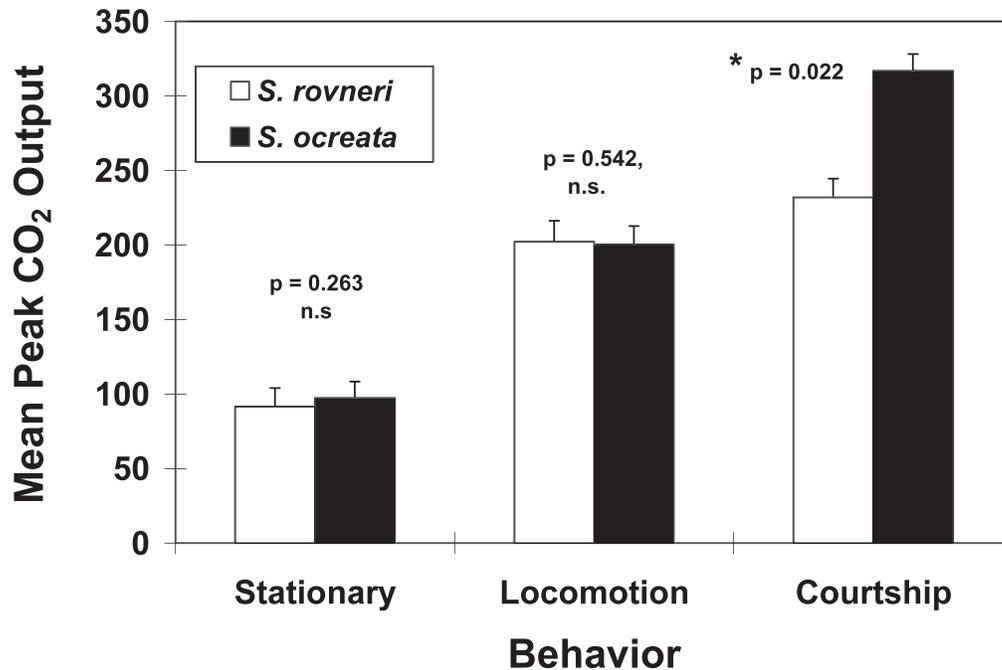


Figure 2.—Mean ( $\pm$  SEM) peak CO<sub>2</sub> output ( $\mu$ l/g/hr) for male *Schizocosa ocreata* ( $n = 7$ ) and *Schizocosa rovneri* ( $n = 6$ ) during bouts of stationary, locomotor, and courtship behavior. Results of pairwise statistical comparisons (Mann-Whitney U-test) between species are indicated. Abbreviations: NS = not significant; \* = significant at  $P < 0.05$ .

(Scheffer et al. 1996; Uetz et al. 2009), which demand greater energy expenditure. The compacted litter substrate of *S. rovneri* transmits seismic vibrations up to 50 cm (Scheffer et al. 1996), allowing use of a less energetically-demanding percussive “body bounce”, to convey signals on this surface.

Differences in courtship vigor also could reflect sexual selection for performance in male signaling, as vigorous courtship display may serve as an “honest indicator” of male condition on multiple levels (Zahavi 1975; Zuk 1991; Kotiaho 2000; reviewed in Byers et al. 2010). For example, highly-active males of the drumming wolf spider *Hygrolycosa rubrofasciata* incur greater energetic expense, but are preferred as mates and produce offspring with higher survival rates than those males displaying less drumming (Mappes et al. 1996; Kotiaho et al. 1996, 1998; Kotiaho 2000; Parri et al. 2002). However, male *H. rubrofasciata* with higher drumming rates also suffer reduced immune function (Ahtianen et al. 2005, 2006). Likewise, males of both *S. ocreata* and *S. rovneri* exhibiting higher signaling rates have greater mating success (Delaney 1997; Delaney et al. 2007; Gibson & Uetz 2008). At the same time, the increased conspicuousness of vigorous male *S. ocreata* signaling may increase detection by visual predators, whereas *S. rovneri* may not (Pruden & Uetz 2004; Roberts et al. 2007). Thus, if signaling traits are indicators of a male’s ability to assimilate, store, and use energy, or indicate higher levels of immune function or viability, a female receiving gametes from these males would obtain genes conferring superior foraging, metabolic and/or immune response abilities for her offspring.

In conclusion, while the active multimodal signaling of *S. ocreata* undoubtedly contributes to increased efficacy of communication within complex environments that constrain particular channels of communication (Scheffer et al. 1996;

Hebets & Papaj 2005), that increased efficacy comes with a higher energetic cost (current study) as well as increased predation risk (Pruden & Uetz 2004; Roberts et al. 2007). Consequently, the energetic expense associated with complex signals used by male *S. ocreata* would therefore represent the basis for multimodal courtship as an “honest indicator” of male quality or condition (Zahavi 1975; Zuk 1991; Ketola & Kotiaho 2009; Byers et al. 2010), and provide indirect fitness benefits as a criterion for female mate choice.

#### ACKNOWLEDGMENTS

We wish to thank Dr. Richard Lee (Miami University, Oxford, Ohio) and lab personnel for access to facilities and guidance in using the Sable respirometry equipment and software. Preparation of this manuscript has benefitted from discussions with Dr. Ken Prestwich (College of Holy Cross) and we appreciate his consultation and advice on methods and respirometry. We thank A. DeLay, E. Hebets, J. Miller, M. Orr, and M. Persons for assistance in collecting and/or rearing the subjects used for this work and the Cincinnati Nature Center at Rowe Woods for letting us collect spiders on their property. We also appreciate editorial comments by L. Higgins and two anonymous reviewers. This work was partially funded by the National Science Foundation (IBN – 9414239, IBN 9906446, IBN 0239164 and IOS1026995 to GWU).

#### LITERATURE CITED

- Ahtianen, J.J., R.V. Alatalo, R. Kortet & M.J. Rantala. 2005. A trade-off between sexual signaling and immune function in a natural population of the drumming wolf spider *Hygrolycosa rubrofasciata*. *Journal of Evolutionary Biology* 18:985–991.
- Ahtianen, J.J., R.V. Alatalo, R. Kortet & M.J. Rantala. 2006. Immune function, dominance and mating success in drumming

- male wolf spiders *Hygrolycosa rubrofasciata*. Behavioral Ecology Sociobiology 60:826–832.
- Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.
- Byers, J., E. Hebets & J. Podos. 2010. Female mate choice based upon male motor performance. Animal Behaviour 79:771–778.
- Delaney, K.J., J.A. Roberts & G.W. Uetz. 2007. Male signaling behavior and sexual selection in a wolf spider (Araneae: Lycosidae): a test for dual function. Behavioral Ecology and Sociobiology 62:67–75.
- Elias, D.O., A.C. Mason & R.R. Hoy. 2004. The effect of substrate on the efficacy of seismic courtship signal transmission in the jumping spider *Habronattus dosseus* (Araneae: Salticidae). Journal of Experimental Biology 207:4105–4110.
- Elias, D.O., A.C. Mason & E.A. Hebets. 2010. A signal-substrate match in the substrate-borne component of a multimodal courtship display. Current Zoology 56:370–378.
- Gibson, J.S. & G.W. Uetz. 2008. Seismic communication and mate choice in wolf spiders: components of male seismic signals and mating success. Animal Behaviour 75:1253–1262.
- Hebets, E.A., K. Cuasy & P.K. Rivlin. 2006. The role of visual ornamentation in female choice of a multimodal male courtship display. Ethology 112:1062–1070.
- Hebets, E.A., D.O. Elias, A.C. Mason, G.L. Miller & G.E. Stratton. 2008. Substrate-dependent signaling success in the wolf spider, *Schizocosa retrorsa*. Animal Behaviour 75:605–615.
- Hebets, E.A. & G.W. Uetz. 1999. Female responses to isolated signals from multimodal male courtship displays in the wolf spider genus *Schizocosa* (Araneae: Lycosidae). Animal Behaviour 57:865–872.
- Hebets, E.A. & G.W. Uetz. 2000. Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 47:280–286.
- Hebets, E.A. & D. Papaj. 2005. Complex signal function: developing a framework of testable hypotheses. Behavioral Ecology and Sociobiology 57:197–214.
- Hebets, E.A. & C.J. Vink. 2007. Experience leads to preference: experienced females prefer brush-legged males in a population of syntopic wolf spiders. Behavioral Ecology 18:1010–1020.
- Ketola, T. & J. Kotiaho. 2009. Inbreeding, energy use and condition. Journal of Evolutionary Biology 22:770–781.
- 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., R.V. Alatalo, J. Mappes, M.G. Nielsen, S. Parri & A. Rivero. 1998. Energetic costs of size and sexual signaling in a wolf spider. Proceedings of the Royal Society B: Biological Sciences 265:2203–2209.
- Kotiaho, J.S., R.V. Alatalo, J. Mappes, M.G. Nielsen, S. Parri & A. Rivero. 2000. Microhabitat selection and audible sexual signaling in the wolf spider *Hygrolycosa rubrofasciata* (Araneae, Lycosidae). Acta Ethologica 2:123–128.
- Kotiaho, J.S., R.V. Alatalo, J. Mappes & S. Parri. 1996. Sexual selection in a wolf spider: male drumming activity, body size, and viability. Evolution 50:1977–1981.
- Leger, D. & I. Didrichsons. 1994. An assessment of data pooling and some alternatives. Animal Behaviour 48:823–832.
- Mappes, J., R.V. Alatalo, J.S. Kotiaho & S. Parri. 1996. Viability costs of condition-dependent sexual male display in a drumming wolf spider. Proceedings of the Royal Society B: Biological Sciences 263:785–789.
- Miller, G.L., G.E. Stratton, P.R. Miller & E. Hebets. 1998. Geographical variation in male courtship behaviour and sexual isolation in wolf spiders of the genus *Schizocosa*. Animal Behaviour 56:937–951.
- Parri, S., R.V. Alatalo, J.S. Kotiaho & J. Mappes. 1997. Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata*. Animal Behaviour 53:305–312.
- Parri, S., R.V. Alatalo, J.S. Kotiaho, J. Mappes & A. Rivero. 2002. Sexual selection in the wolf spider *Hygrolycosa rubrofasciata*: female preference for drum duration and pulse rate. Behavioral Ecology 13:615–621.
- Paul, R. & H. Storz. 1987. On the physiology of the hemolymph of arachnids. Verhandlungen der Deutschen Zoologischen Gesellschaft 80:221.
- Prestwich, K.N. 1983. The roles of aerobic and anaerobic metabolism in active spiders. Physiological Zoology 56:122–132.
- Prestwich, K.N. 1988a. The constraints on maximal activity in spiders. I. Evidence against the hydraulic insufficiency hypothesis. Journal of Comparative Physiology 158B:437–447.
- Prestwich, K.N. 1988b. The constraints on maximal activity in spiders. II. Limitations imposed by phosphagen depletion and anaerobic metabolism. Journal of Comparative Physiology 158B:449–456.
- Pruden, A.J. & G.W. Uetz. 2004. Assessment of potential predation costs of male decoration and courtship display in wolf spiders using video digitization and playback. Journal of Insect Behavior 17:67–80.
- Rivero, A., R.V. Alatalo, J.S. Kotiaho, J. Mappes & S. Parri. 2000. Acoustic signaling in a wolf spider: can signal characteristics predict male quality? Animal Behaviour 60:187–194.
- Roberts, J.A. & G.W. Uetz. 2004a. Chemical signaling in a wolf spider: a test of ethosppecies discrimination. Journal of Chemical Ecology 30:1271–1284.
- Roberts, J.A. & G.W. Uetz. 2004. Species-specificity of chemical signals: silk source affects discrimination in a wolf spider (Araneae: Lycosidae). Journal of Insect Behavior 17:477–491.
- Roberts, J.A., P.W. Taylor & G.W. Uetz. 2007. Consequences of complex courtship display: predator detection of multimodal signaling. Behavioral Ecology 18:236–240.
- Scheffer, S.J., G.W. Uetz & G.E. Stratton. 1996. Sexual selection, male morphology, and the efficacy of courtship signaling in two wolf spiders (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 38:17–23.
- Stratton, G.E. 2005. Evolution of ornamentation and courtship behavior in *Schizocosa*: insights from a phylogeny based on morphology (Araneae: Lycosidae). Journal of Arachnology 33:347–376.
- Stratton, G.E. & G.W. Uetz. 1981. Acoustic communication and reproductive isolation in two species of wolf spiders. Science 214:575–577.
- Stratton, G.E. & G.W. Uetz. 1986. The inheritance of courtship behavior and its role as a reproductive isolating mechanism in two species of *Schizocosa* wolf spiders (Araneae: Lycosidae). Evolution 40:129–141.
- Uetz, G.W. & G. Denterlein. 1979. Courtship behavior, habitat, and reproductive isolation in *Schizocosa roveri* (Uetz and Dondale) (Araneae: Lycosidae). Journal of Arachnology 7:86–88.
- Uetz, G.W., R. Papke & B. Kilinc. 2002. Influence of feeding regime on male secondary sexual characters in *Schizocosa ocreata* (Hentz) wolf spiders (Araneae: Lycosidae): evidence for condition-dependence in a visual signaling trait. Journal of Arachnology 30:461–469.
- Uetz, G.W. & J.A. Roberts. 2002. Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. Brain, Behavior and Evolution 59:222–230.
- Uetz, G.W., J.A. Roberts & P.W. Taylor. 2009. Multimodal communication and mate choice in wolf spiders: female responses to multimodal vs. unimodal male signals in two sibling wolf spider species. Animal Behaviour 278:299–305.
- Zahavi, A. 1975. Mate selection—a selection for a handicap. Journal of Theoretical Biology 53:205–214.
- Zuk, M. 1991. Sexual ornaments as animal signals. Trends in Ecology & Evolution 6:228–231.