

Evolutionarily costly courtship displays in a wolf spider: a test of viability indicator theory

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The costs of secondary sexual traits are crucial to our understanding of sexual selection. Although it is broadly accepted that sexual traits are indirectly or directly costly to express, few studies have quantified such costs. Thus, it is unclear if costs are evolutionarily meaningful and to what degree. Costs play a key role in viability indicator models, which assume that 1) the expression of sexual traits reduces the fitness of the trait bearer, 2) sexual trait expression is dependent on condition, and 3) the costs of sexual trait expression are borne differentially, that is, they are less for individuals in good condition. Using 2 syntopic species of wolf spiders, we addressed the importance of direct predation costs on the viability indicator mechanism. *Pardosa milvina* is a small wolf spider that has conspicuous male courtship behaviors in the form of front leg raises. *Hogna helluo* is a large species that preys on *P. milvina*. In laboratory experiments, we discovered that predation risk from *H. helluo* was higher for courting *P. milvina* males than noncourting males, male *P. milvina* manipulated to be in good condition courted at higher rates than males manipulated to be in poor condition, and males in good condition survived predation risk better than males in poor condition. Our study suggests that predation is a significant, evolutionary cost that can satisfy viability indicator mechanism assumptions. *Key words*: costs, courtship, Lycosidae, predation, sexual selection, spider. [*Behav Ecol* 19:974–979 (2008)]

The costs of elaborate sexual traits (e.g., ornaments, courtship behaviors, calls, and other signals) are of paramount importance to our understanding of sexual selection and remain an issue of great contemporary interest. Currently favored theoretical models for sexual selection assume that sexual traits are costly to produce, and costs play a particularly prominent role in viability indicator (good genes) theory (Williams 1966; Zahavi 1975, 1977; Andersson 1982; Nur and Hasson 1984; Pomiankowski 1987; Grafen 1990a, 1990b; Iwasa et al. 1991; Johnstone and Grafen 1992; Rowe and Houle 1996; Kotiaho 2001; Hausken and Hirshleifer 2004), which has several assumptions: 1) the costs of sexual traits reduce fitness (Grafen 1990a; Johnstone and Grafen 1992); 2) the expression of sexual traits is contingent on phenotypic or genotypic condition (Andersson 1986; Grafen 1990a; Rowe and Houle 1996); and 3) the costs of sexual traits are borne differentially, that is, they are less for individuals in good condition (Grafen 1990a; Rowe and Houle 1996; Tomkins et al. 2004). If the above conditions are satisfied, it is predicted that the degree to which the sexual trait is expressed will be positively correlated with the overall genetic quality of the trait bearer (Kotiaho 2000). A meta-analysis of male sexual trait expression and adult survival provides partial support for some of the above assumptions: data from 69 studies representing a wide range of animal taxa revealed that, in general, males with larger ornaments, larger overall size, and/or higher rates of courtship experienced greater survivorship or longevity (Jennions et al. 2001). These findings are consistent with the idea that male investment in sexually selected traits varies with the individual's ability to pay the underlying costs of expression; thus, trait expression is condition dependent and functions as an honest indicator of quality.

The degree to which sexual traits are expressed is likely to be curbed by the costs of producing them (Darwin 1871). These costs play an important role in viability indicator models and take the form of high energy demands and other mechanisms that tax the physiology of the individual (Kotiaho 2001; Ahtiainen et al. 2005; Sullivan and Kwiatkowski 2007). Most studies of the costs of sexual traits have focused on the first assumption of viability indicator theory. For example, male wolf spiders (*Hygrolycosa rubrofasciata*) induced to drum (= acoustic sexual signal) at higher rates suffer shorter life span (Kotiaho 2000). Also, individuals expressing sexual traits may bear higher predation costs. Predators often exploit the sexual traits of their prey in order to locate them (e.g., Sakaluk and Bellwood 1984; Lima and Dill 1990; Lehmann and Heller 1998; Zuk and Kolluru 1998; Sullivan and Kwiatkowski 2007). For instance, brightly colored male guppies (*Poecilia reticulata*) attract female conspecifics but suffer higher predation levels from blue acara cichlids (*Aequidens pulcher*) than drab males (Godin and McDonough 2003). Sexual traits may also impose handicaps that limit the signaller's ability to escape (Andersson 1994). In all cases, if the costs of sexual traits are to be construed as evolutionarily meaningful, it is critical that we demonstrate that their expression reduces survival and/or reproductive success. Although it is broadly accepted that sexual traits incur indirect or direct costs, there is a paucity of studies that have quantified such costs (Kotiaho 2001). To our knowledge, only one published study has attempted to explore whether predation may act as a condition-dependent cost that ensures honest sexual signalling (i.e., satisfies viability indicator theory assumptions): Lindström et al. (2006) discovered that male wolf spiders (*H. rubrofasciata*) that signalled at high rates incurred greater predation costs when they were not allowed to escape from attacks by experienced pied flycatchers (*Ficedula hypoleuca*). This study also revealed that the risk of predation increased in proportion to the signalling rate, which does not fulfill the assumption that costs are borne differentially. However, when males were given the opportunity to escape, those with higher mobility were best at

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escaping predation attempts, and initial observations suggested that mobility and drumming rate were positively correlated. Although condition was not manipulated in the study of Lindström et al. (2006), their results provide some evidence that predation costs promote honest signalling and may satisfy viability indicator model assumptions, but further investigation is needed.

Using a wolf spider with a conspicuous sexual display, we tested the assumptions that underlie the viability indicator model in a laboratory experiment. Specifically, it was our intent to test if 1) courting males were exposed to higher rates of predation than noncourting males, 2) the intensity of courtship was condition dependent such that males in good condition would court more vigorously than those in poor condition, and 3) males in good condition were better able to escape predation than males in poor condition.

MATERIALS AND METHODS

Study system

Wolf spiders (Araneae: Lycosidae) provide good model organisms for studies of the potential costs of sexual signals and the validity of viability indicator models: they are abundant and easy to rear; are amenable to manipulative laboratory experiments; and have conspicuous, quantifiable courtship displays. In the Midwestern United States, the wolf spiders *Pardosa milvina* and *Hogna helluo* are syntopic, cursorial predators that live in agricultural and early successional habitats, and they often reach high densities (Marshall et al. 2000, 2002). *Pardosa milvina* is a relatively small species (ca., 20–30 mg), and when in the presence of adult females or female cues, adult males engage in conspicuous courtship displays that include repeated front leg raises (Rypstra et al. 2003). *Hogna helluo* is a relatively large species (ca., 300–800 mg) that preys on *P. milvina* (Persons et al. 2001). Much is known about the mating and predatory behaviors of these co-occurring species (e.g., Persons and Rypstra 2001; Persons et al. 2001, 2002; Barnes et al. 2002; Walker and Rypstra 2003; Lehmann et al. 2004; Taylor et al. 2005; Bell et al. 2006), and because wolf spider visual systems are particularly sensitive to movement (e.g., Rovner 1996), the leg raises of courting male *P. milvina* may heighten their predation risk if they are in close proximity to *H. helluo* (e.g., Pruden and Uetz 2004) or another visually acute predator.

Collection and maintenance of spiders

All *P. milvina* used in our study were collected as juveniles from Miami University's Ecology Research Center (Oxford, Butler County, OH) during the fall of 2005 and raised to adulthood in the laboratory. We maintained spiders individually in 5.5-cm high \times 5.5-cm diameter clear, cylindrical plastic containers adding a 2-cm layer of moistened peat moss as a substrate to minimize risks of desiccation. *Pardosa milvina* were reared on a diet of 2 domestic crickets (2 mm; *Acheta domesticus*) twice a week, and peat moss substrates were watered regularly. *Hogna helluo* involved in our study were the first-generation offspring of adult females previously collected from the Ecology Research Center. We maintained them in 8-cm high \times 5.5-cm diameter cylindrical white plastic cups with clear lids. A 2-cm layer of moistened peat moss was added as a substrate to allow for their natural burrowing behavior and to prevent desiccation. We fed *H. helluo* appropriately sized domestic house crickets twice a week when they were juvenile and once a week as adults. All containers with spiders were housed in an environmental chamber with a relative humidity near 70%, a photoperiod of 13:11 light:dark, and a temperature of approximately 25 °C.

General experimental protocol

After the maturation of *P. milvina*, we randomly assigned 91 adult males to one of 2 condition groups: a poor condition group ($n = 46$) and a good condition group ($n = 45$). Males assigned to the poor condition group were fed one 2-mm cricket twice a week, and males assigned to the good condition group were fed four 2-mm crickets twice a week. We maintained all male *P. milvina* on their respective diet regimes for 3 weeks. Subsequently, we randomly assigned all males to one of 3 trial groups: a courtship only group, a predation risk and courtship group, and a predation risk only group. The courtship only group involved placing an adult male *P. milvina* in an arena (described below) with an adult virgin female *P. milvina*. Female *P. milvina* in this group were allowed to deposit cues (silk, excreta, and associated pheromones) on a filter paper substrate in the arena for 1 h before trials began, as substrate-borne cues are important for eliciting male courtship behaviors (Rypstra et al. 2003). After 1 h of cue deposition, we corralled female *P. milvina* in the center of the arena under an overturned glass vial (8-cm high \times 2-cm diameter) and introduced the male. Male *P. milvina* could thus respond to both visual and putative chemotactile cues from female conspecifics, but they could not interact with them physically. The predation risk and courtship group was treated like the courtship only group; however, we also placed an adult female *H. helluo* that had been sated and subsequently starved for 7 days into the arena along with the introduction of the male. Female *P. milvina* were protected from predation by *H. helluo* under their glass vials throughout the duration of trials, as we were interested in the potential predation costs of male courtship only. The predation risk only group involved placing an adult male *P. milvina* in an arena with a starved adult female *H. helluo*. An empty, overturned glass vial (8-cm high \times 2-cm diameter) was placed in the center of the arena. We initially placed male *P. milvina* and female *H. helluo* (if present) in arenas and covered each spider with an overturned plastic vial (9.5-cm high \times 4-cm diameter). The spiders remained under the vials during a 5-min acclimation period. After this period, we removed the vials housing male *P. milvina* and female *H. helluo* and allowed them to interact freely for 30 min or until either predation occurred or the male *P. milvina* escaped the arena via a small exit hole in the trial arena (Figure 1). Spiders were used once in trials. All statistical analyses were performed using JMP 5.1 statistical software.

Trial arena and data collection

We built and used trial arenas constructed from 2 plastic containers: a small, inner cylindrical plastic container (7.75-cm high \times 19-cm diameter) fit inside a larger, outer cylindrical plastic container (8-cm high \times 20.5-cm diameter). In the smaller container, we poured 250 mL of DAP Plaster of Paris to create smooth, level floors. In addition, we drilled one 0.5-cm diameter circular hole in the side of the smaller container such that the base of the hole was flush with the plaster floor. This hole gave adult male *P. milvina* but not adult female *H. helluo* the opportunity to escape the smaller container (and enter the larger container) (Figure 1). Before trials began, we placed a piece of Whatman Filter Paper on the plaster floor to serve as a substrate. Some arenas were used more than once during the course of our experiment, and we washed reused arena containers thoroughly in warm soapy water and rinsed them with 95% ethanol to remove residual chemical cues from spiders. We placed arenas in an isolated booth under a Panasonic WV-CP470 video camera located in an environmentally controlled room. The camera was connected to a GOVIDEO R6740 DVD recorder located in a nearby

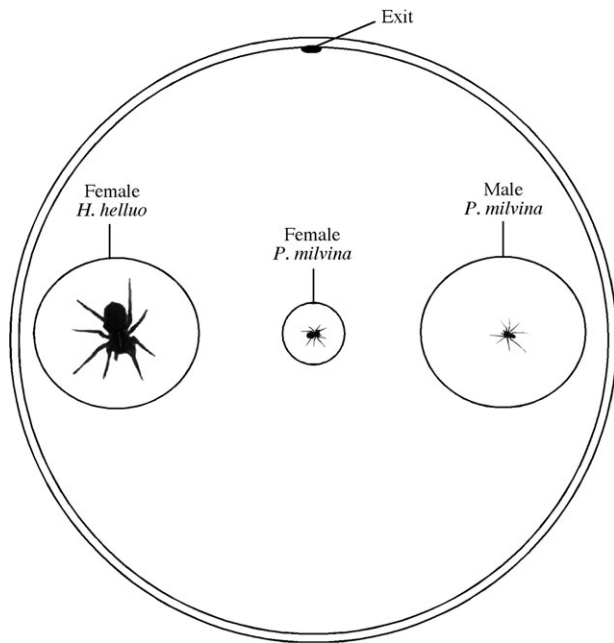


Figure 1

Experimental arena comprised of an inner container with exit hole and a larger outer container. Female *Pardosa milvina* (if used) were placed under a glass vial in the center of the arena. Female *Hogna helluo* (if used) and male *P. milvina* were initially placed under vials for 5 min at opposite ends of the arena and were subsequently released for 30-min trials.

laboratory room. We video recorded all 30-min trials over a period of 8 days and later scored them by recording the number of male *P. milvina* leg raises and courtship rate (=leg raises per minute) for trials including female *P. milvina* (predation risk and courtship treatment and courtship only treatment) and whether males survived predation risk in trials including female *H. helluo* (predation risk and courtship treatment and predation risk only treatment).

At the end of our experiment, we randomly selected 15 males from both diet regimes and measured body condition (a measure of physiological state that is size independent) using the residual index (Jakob et al. 1996). For males in the poor condition and good condition treatments, we measured abdomen width (a flexible trait that increases as a function of feeding) and carapace width (an inflexible trait not affected by food intake throughout the duration of an instar) using a digital ocular micrometer mounted on a dissecting microscope. We regressed \ln (abdomen width) on \ln (carapace width) and compared the residuals for each treatment using a 2-sample *t*-test.

RESULTS

Male condition

Adult male *P. milvina* assigned to the good condition group were in significantly better condition than males assigned to the poor condition group (*t* ratio = -12.99, $P < 0.0001$, $n = 30$) (Figure 2).

Testing viability indicator theory assumptions

Assumption 1: sexual traits have fitness costs

To test the first assumption of viability indicator theory, we compared the survival of male *P. milvina* (good condition

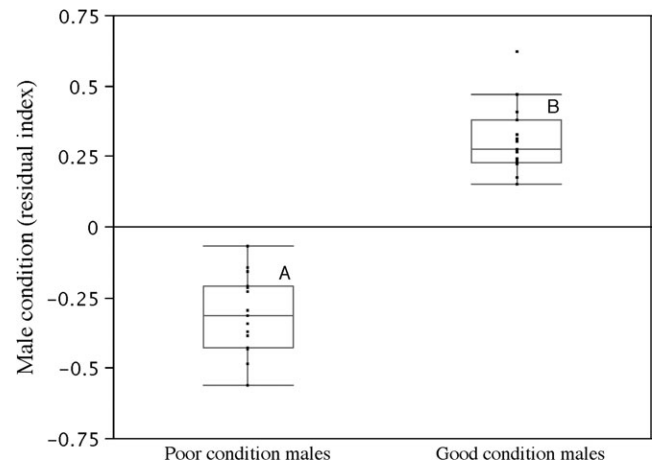


Figure 2

Mean condition of males (\pm standard deviation) taken from samples assigned to good condition and poor condition feeding regimes.

and poor condition) assigned to the predation risk and courtship treatment with males assigned to the predation risk only treatment. Males only exhibited leg raises (i.e., expressed the sexual trait) in trials with female conspecifics, and all males expressed the sexual trait in trials with female conspecifics. We made comparisons of survival distributions using a Kaplan–Meier model survival regression analysis. Specifically, we used the nonparametric 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.

For male *P. milvina* in poor condition, courtship had a significant effect on predation by *H. helluo*: courting males (predation risk and courtship treatment) had significantly lower survivorship than noncourting males (predation risk only treatment) (Mantel–Cox, $\chi^2 = 20.25$, $P < 0.0001$, $n = 31$). Similarly, in trials involving males in good condition, courtship had a significant effect on predation: courting males had significantly lower survivorship than noncourting males (Mantel–Cox, $\chi^2 = 10.6$, $P = 0.0049$, $n = 31$) (Figure 3).

Assumption 2: sexual trait expression is condition dependent

To test the second assumption of viability indicator theory, we compared the courtship rate (leg raises per minute) of male *P. milvina* between males in poor and good condition. We made this comparison in the courtship only treatment and the predation risk and courtship treatment. Because data were not normally distributed, we made comparisons via Mann–Whitney *U* tests.

When no predators were present, male *P. milvina* in good condition courted at significantly higher rates than males in poor condition (Mann–Whitney *U* test, $Z = 4.52$, $P < 0.0001$, $n = 29$). Likewise, for males assigned to the predation risk and courtship treatment, males in good condition courted at significantly higher rates than males in poor condition (Mann–Whitney *U* test, $Z = 2.04$, $P = 0.042$, $n = 31$) (Figure 4). Interestingly, males in poor condition courted more in the presence of a predator than in treatments with no predator present (Mann–Whitney *U* test, $Z = -2.34$, $P = 0.0194$, $n = 31$). This was not the case for males in good condition: those in the courtship only treatment courted at significantly higher rates than males in the predation risk and courtship treatment (Mann–Whitney *U* test, $Z = 2.31$, $P = 0.021$, $n = 29$) (Figure 4).

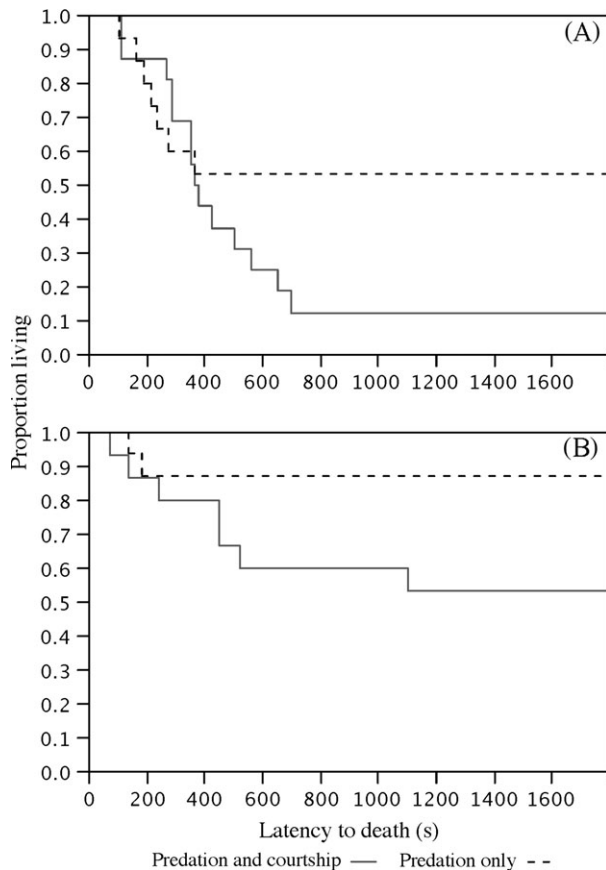


Figure 3 Kaplan-Meier survival function in the predation risk and courtship treatment and the predation risk only treatment for male *Pardosa milvina* in (A) poor condition and (B) good condition. Male *P. milvina* in both poor and good condition had a significantly lower survivorship in the predation risk and courtship treatment than the predation risk only treatment.

Assumption 3: costs of sexual traits are less for males in good condition

To test the third assumption of viability indicator theory, we compared survival distributions of males in good and poor condition in the predation risk and courtship treatment. As in Assumption 1, we used Kaplan-Meier survival regression analysis to make survivorship comparisons.

Courting male *P. milvina* in good condition had higher survivorship than courting males in poor condition (Mantel-Cox, $\chi^2 = 5.6$, $P = 0.018$, $n = 31$) (Figure 5).

DISCUSSION

Results from our study demonstrate that courtship in male *P. milvina* wolf spiders is a clear indicator of quality: courtship reveals information about condition, which is associated with the ability to escape predation from the larger, syntopic wolf spider *H. helluo*. In our study, we discovered that courting male *P. milvina* males suffered greater mortality from predation than noncourting males that were subjected to a real predation risk. This pattern applied to males that were in both good and poor condition. These results satisfy the first assumption of viability indicator models that sexual traits reduce an individual's fitness and are consistent with previous findings. For example, the acoustically orienting parasitoid fly *Therobia leonidei* uses the trills (= sexual signal) of male bush-

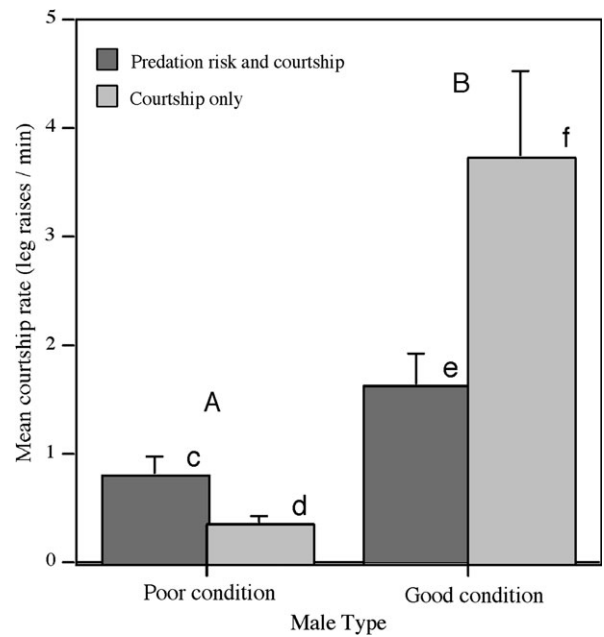


Figure 4 Average courtship rate (leg raises per minute) of male *Pardosa milvina* in poor and good condition assigned to the predation risk and courtship treatment and the courtship only treatment. Males in good condition courted at significantly higher rates than males in poor condition.

crickets (*Poecilimon propinquus*) to locate them as hosts (Lehmann and Heller 1998), and the jumping spider *Phidippus clarus* uses visual information to hunt courting wolf spiders (*Schizocosa ocreata*) but responds more quickly if multimodal information (visual and seismic sexual signals) is available (Roberts et al. 2007).

Viability indicator models of sexual selection assume that sexually selected traits are evolutionarily costly and are expressed proportionally to the condition of the trait bearer (Zahavi 1977; Johnstone 1995; Kotiaho 2000; Hausken and Hirschleifer 2004). Thus, sexual traits may act as honest indicators of qualities important to the choosier sex. As Kotiaho

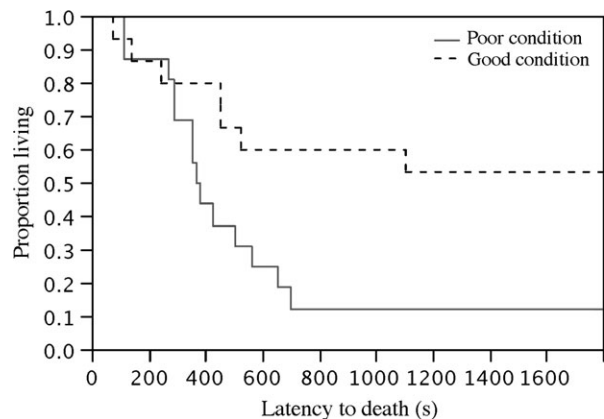


Figure 5 Kaplan-Meier survival function in the predation risk and courtship treatment for male *P. milvina* in poor and good condition. Males in good condition had significantly greater survivorship than males in poor condition.

(2001) points out, despite numerous studies suggesting that sexual traits increase risks of predation (e.g., Baker and Bibby 1987; Petrie 1992; Slagsvold et al. 1995; Huhta et al. 2003), very few studies have attempted to quantify these costs, and to our knowledge, this study is the first attempt to test whether predation is a significant, evolutionary cost that can satisfy viability indicator mechanism assumptions by simultaneously manipulating condition and the sexual trait. Results from our study indicate that conspicuous courtship behaviors in the form of leg raises in adult male *P. milvina* wolf spiders incur direct fitness costs via predation by *H. helluo*. However, these costs are borne differentially and are less for males in good condition. Our study not only corroborates the generally accepted paradigm that sexual traits are costly but also demonstrates that predation can be a significant, evolutionary cost that satisfies viability indicator mechanism assumptions.

It is important to consider the potentially confounding variable of female *P. milvina* cues (e.g., pheromones, silk, excreta, etc.) that were present in the predation risk and courtship treatment trials but not in trials involving a predation risk only. These cues may have primed the hunting behaviors of *H. helluo* and put male *P. milvina* under a heightened predation risk, as some wolf spiders, including *H. helluo*, have been shown to respond to the chemical cues of their prey (e.g., Persons and Uetz 1996; Persons and Rypstra 2001; Hoefler et al. 2002). However, Persons and Rypstra (2000) demonstrated that *H. helluo* only exhibit foraging biases in behavior for prey for which they have had experience. The *H. helluo* involved in our study were raised on a diet that did not include *P. milvina*, which likely minimized the differences in predation risk between the 2 treatments.

The second prediction of viability indicator models is that sexual trait expression is condition dependent. Results from our study are consistent with this assumption: male *P. milvina* in good condition courted females at significantly higher rates than males in poor condition. This was true for trials in which there was and was not a risk of predation. Males in good condition courted females at significantly higher rates when there was no predation risk from *H. helluo*. This may indicate that males in good condition act more cautiously toward predation risk to compensate for their increased rates of courtship and thus conspicuousness, as has been discovered in field crickets (Hedrick 2000). Conversely, males in poor condition courted females at significantly higher rates when under a real predation risk than when there was no risk of predation. This might suggest that condition affects how males weigh the benefits of mating versus the potential predation costs of courtship, and males in poor condition may take higher predation risks in order to attract prospective mates.

Our results do not entirely agree with previous studies of the effects of predation risk on courtship rate in *P. milvina*. Taylor et al. (2005) demonstrated that male *P. milvina* courtship rate was not affected by predation risk from *H. helluo*; however, the design of their study differed from ours in potentially important ways. Substratum-borne cues from *H. helluo* were used as a proxy for predation, that is, there was not an actual predator present. In addition, *H. helluo* were allowed to deposit cues on filter paper for 24 h before trials began in the study of Taylor et al. (2005), whereas substrate-borne predator cues in our study could have only been laid down during the course of a trial. Results from our study accord with the suggestion of Taylor et al. (2005) that the addition of visual and/or vibrational cues from a real predator may induce modulation of the conspicuous courtship displays of male *P. milvina*, as has been found in other species (e.g., Hedrick 2000).

The combined findings that male *P. milvina* in good condition had significantly greater survivorship than males in poor condition and that males in good condition courted at a

significantly higher rate than males in poor condition strongly suggest that the costs of male sexual display are less for males in good condition. These findings also satisfy the third assumption of viability indicator models. Thus, male courtship in the form of leg raises is a costly trait that appears to be a reliable, condition-dependent sign of male quality. Reproductive benefits may offset the costs of vigorous courtship, as previous studies have shown that female *P. milvina* are more likely to mate with males that court at high rates (Rypstra et al. 2003).

It is important to acknowledge that our study was entirely laboratory based; thus, demonstrable evidence of evolutionarily meaningful costs of courtship under natural conditions is still needed. However, our study remains relevant to real biological processes. For example, the primary predators of spiders are other spiders (Foelix 1996), and spider body condition (including *P. milvina* condition) ranges widely in the field (Jakob et al. 1996). It is also important to note that we manipulated spider phenotypic and not genotypic condition. Although genetically superior males are, on average, likely to be in better phenotypic condition, this would be a fertile area to explore in future studies.

In conclusion, results from our laboratory study provide compelling evidence for viability indicator models: male *P. milvina* that courted via leg raises were more likely to be preyed on by *H. helluo* than males that did not court, males in good condition courted at higher rates than males in poor condition, and males in good condition had greater survivorship than males in poor condition. To determine with a greater degree of certainty whether leg raises evolved as costly indicators of heritable qualities, it would be valuable to determine if adult females derive indirect benefits from males that naturally court at high rates.

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