

Female preference for complex/novel signals in a spider

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Identifying the various factors that influence complex signal evolution is a difficult task, yet it is fundamental to understanding the evolution of animal communication. Here we explore the evolution of complex courtship signaling by taking advantage of a system in which sexual selection on male courtship traits has driven the diversification of geographically isolated populations of the jumping spider *Habronattus pugillis* Griswold. Using 2 populations (Santa Rita [SR] and Atascosa [AT]) in which SR females show xenophilic mating preferences for foreign (AT) over local males (SR), we examine the mechanisms driving this preference. Both AT and SR males produce multimodal signals (visual + seismic), and while SR and AT signals share certain seismic components, AT seismic signals are more complex and contain novel components. We conducted mate choice trials where SR females were presented with AT or SR males that were either muted or nonmuted. SR females preferred to mate and mated more quickly with foreign AT males over local SR males only if AT males could produce seismic signals (nonmuted treatment). In addition, we found that SR females spent a higher proportion of time attentive to foreign AT males only if they could produce seismic signals. This evidence suggests that SR females have a bias for complex and/or novel forms of seismic signals. *Key words*: antagonistic co-evolution, complex signaling, female choice, multimodal signaling, novelty, spider. [*Behav Ecol*]

Identifying female mating preferences and the male signals on which those preferences are based on is an integral part of studying animal communication, yet is especially challenging in animals where males transmit multiple signals in multiple modalities. Different male signals may be under different selective pressures and may interact in complex nonadditive ways leading to complex patterns in mating preferences (Pomiankowski and Iwasa 1993, 1998; Iwasa and Pomiankowski 1994; Partan and Marler 1999, 2005; Rowe 1999; Candolin 2003; Hebets 2005; Hebets and Papaj 2005). Recognizing male signals and female preferences is an essential step in analyzing mechanisms of behavior and in disentangling different models of sexual selection.

Studies on female mating preferences most often involve looking at mate choice based on male signals with some naturally occurring variation (Andersson 1994). Such studies are important in assessing signal function and when combined with other information (i.e., signaling and receiving costs, measurements of male quality, and mating costs) can be informative in assessing different models of sexual selection (Ryan 1990; Andersson 1994; Endler and Basolo 1998; Holland and Rice 1998; Chapman et al. 2003; Hebets and Maddison 2005; Rowe et al. 2005). An alternative method of assessing female preferences is to observe female responses to male signals that do not necessarily occur in natural populations. Such a paradigm is especially relevant in exploring female biases and may give hints as to underlying physiological processes, environmentally imposed signaling and processing constraints, and the evolutionary processes involved in mate choice and signal evolution (Basolo 1990, 1998; Endler 1992, 1993; Ryan and Rand 1993, 2003; McClintock and Uetz 1996; Endler and Basolo 1998; Hebets and Uetz 2000). These types

of experiments are usually done by synthetically varying different qualities of male signals and observing female responses (Ryan and Keddyhector 1992; Andersson 1994; McClintock and Uetz 1996; Rosenthal 1999; Hebets and Uetz 2000; Gerhardt and Huber 2002; Guerra and Morris 2002) or in systems where male signals show large geographical variation, performing reciprocal mating crosses with males from foreign and local populations (Houde and Endler 1990; Basolo 1998; Jones and Hunter 1998; Ptacek 1998; Hamilton and Poulin 1999; Gray and Cade 2000; Hebets and Maddison 2005).

Jumping spider (Salticidae) courtship displays have proved to be fruitful models in studying behavior and sexual selection. Male jumping spiders, unlike females, have evolved conspicuously ornamented and colored appendages that they wave like semaphores during courtship, producing stereotyped, species-specific visual displays (Crane 1949; Jackson 1982; Forster 1982b; Elias et al. forthcoming) that are thought to function in species isolation, species recognition, and female choice (Jackson 1982; Richman 1982; Forster 1982b; Clark and Uetz 1993; Maddison and McMahon 2000; Taylor et al. 2000; Clark and Morjan 2001; Clark and Biesiadecki 2002). *Habronattus pugillis* is a jumping spider that occurs in isolated woodland habitats atop mountain ranges (sky islands) throughout southeastern Arizona. Male *H. pugillis* are typified by sexual ornaments, morphologies, locomotory, and seismic courtship displays that differ dramatically between mountain ranges, whereas phenotypic uniformity exists within mountain ranges (Maddison and McMahon 2000; Elias et al. forthcoming). Using a combination of molecular, phylogenetic, behavioral, and phylogeographic data, it has been demonstrated that sexual selection is driving this diversification among mountain populations of *H. pugillis* (Maddison and McMahon 2000; Masta 2000; Masta and Maddison 2002).

Experiments using reciprocal mating trials between 2 populations of *H. pugillis* (Santa Rita [SR] and Atascosa [AT]) recently demonstrated asymmetric mating preferences, in which females from 1 population (SR) preferred foreign males to their own local males (Hebets and Maddison

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2005). Females that preferred foreign males spent more time being visually attentive to foreign male courtship than to local male courtship, and this difference in visual attention did not appear to be directly related to differences in visually based signals between the 2 populations (Hebets and Maddison 2005). The authors suggested that the preferred AT males may have a component to their courtship that is extremely attractive and proposed that this component may involve a seismic signal (Hebets and Maddison 2005). In a later study, Elias et al. (forthcoming) described seismic displays from 7 *H. pugillis* populations and found differences in the complexity of seismic signals between populations, measured as the number of separate components that made up each display. AT seismic displays were the most complex, consisting of 3 components, whereas SR seismic displays were the simplest, consisting of a single component. In combination, results from both studies suggest that SR females may have a preference for complex/novel seismic signals.

Here, we directly test whether female biases for complex/novel seismic signals are driving the observed preference among SR females for foreign AT males. We manipulated AT and SR males into muted and nonmuted treatments and conducted mate choice trials with SR females. We found that muting AT males resulted in a reduced preference by SR females. SR females preferred and were more visually attentive to AT males only if they could produce the complex AT seismic display, suggesting that SR females are more attracted to a complex/novel form of seismic courtship signals.

METHODS

Spiders

Male and immature female *H. pugillis* were collected from different mountain ranges in Arizona in April 2003 and 2004 (males—Atascosa Mountains; male and females—Santa Rita Mountains). Experiments were conducted May–July 2003 and May–June 2004 with animals caught in the same calendar year. Males and females were kept isolated from each other after field collection. Animals were housed individually in plastic containers (AMAC Plastic Products, Petaluma, California) and kept in the laboratory on a 12:12 h light:dark cycle. Once a week, spiders were fed fruit flies (*Drosophila melanogaster*) and juvenile crickets (*Acheta domesticus*).

Behavioural traits of *H. pugillis*

We recorded seismic signals from courting males using a laser vibrometer (Elias et al. 2003, forthcoming). Below are descriptions of courtship behavior of the males used in the study. For more detailed descriptions, see Elias et al. (forthcoming) and Maddison and McMahon (2000).

AT males

AT male faces are covered with silver-gray scales, except for the lower lateral portions that are yellowish with dark spots (Maddison and McMahon 2000). The sides of the carapace are swollen. There is no eye streak above their anterior eyes, as seen in SR males (see below), and the chelicerae are striped. The locomotory courtship consists of rapid sidling, which involves moving back and forth in large arcs in front of the female with the first pair of legs held above the ground the entire time (Maddison and McMahon 2000). After sidling, males approach females with vigorous flicking of the forelegs. Seismic signals are produced during leg flicking and not during the sidling display. Every leg flick is coordinated with a seismic signal. AT male seismic displays are relatively long in duration and occur in 3 distinct parts (Figure 1). The first part consists of a short, high-intensity, broadband “crackle”

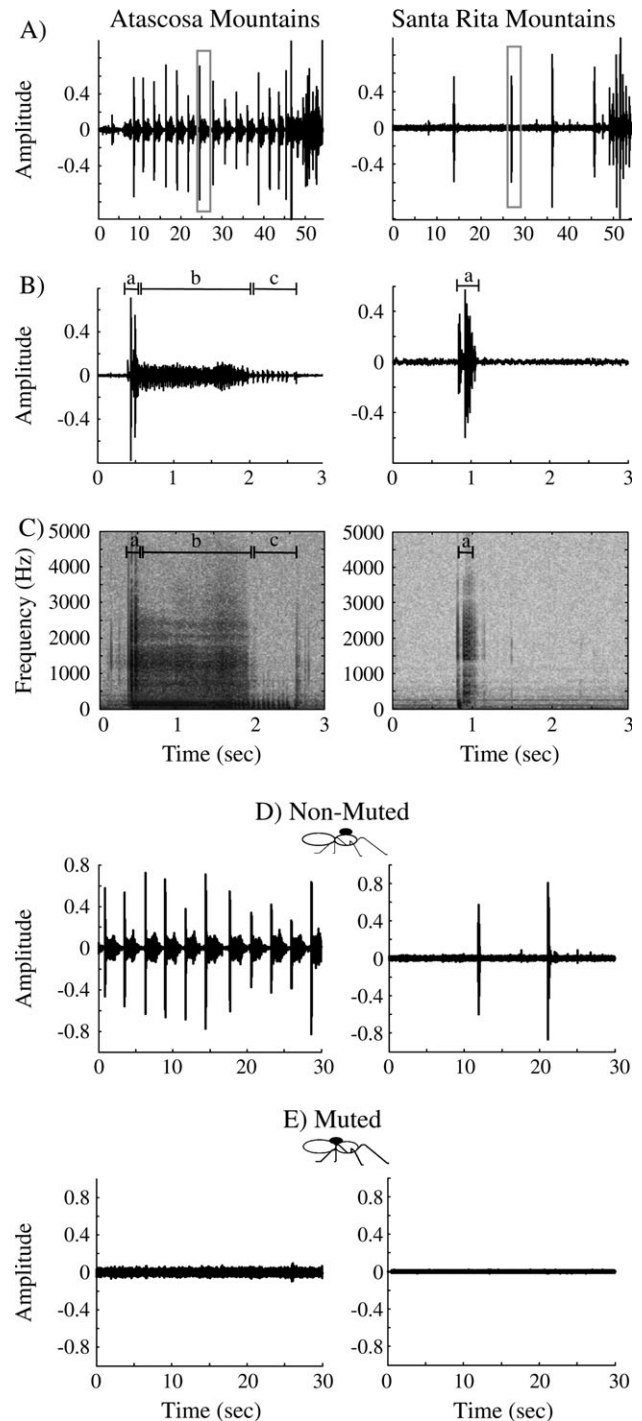


Figure 1

Seismic signals of *Habronattus pugillis* from the AT and SR mountain populations. (A) Oscillograms of seismic sounds. (B) Detail of oscillogram (red box in part A). (C) Spectrogram of seismic signal in part B. a–c denote the 3 seismic components of male courtship signals (a, crackle; b, rasp; and c, drone). Males produce seismic sounds during courtship, and different populations produce different seismic displays. (D and E) Effects of experimental manipulation on *H. pugillis* seismic signals. (D) Representative male seismic signals from both populations with wax placed on top of the prosoma (control, nonmuted). (E) Representative male seismic signals from both populations with wax connecting the cephalothorax to the abdomen (experimental treatment, muted). Waxing the cephalothorax to the abdomen removes all seismic signals.

(*a* in Figure 1c). The second part consists of a prolonged long duration, broadband “rasp” (*b* in Figure 1c) (combined with “drones”—see below). The third part consists of variable bouts of short duration, broadband drones (*c* in Figure 1c). Broadband drones also occur along with rasps in the second courtship stage (*b* in Figure 1c) but are lower in intensity than rasps.

SR males

SR male faces are dark brown with a white horizontal stripe along the bottom (Maddison and McMahon 2000). They have a thin streak of white scales that extends above their anterior eyes. The anterior-most pair of walking legs also has pendant fringes of hair. The courtship behavior of these males begins with rotations of the palps (modified appendages beside the face) (Maddison and McMahon 2000). This palpal rotation is unique to SR males and is continued throughout the courtship display. Palp rotations are often punctuated with rapid flicks of the forelegs. Males remain mostly stationary during courtship until the actual approach to the female, which is generally direct. The final stages of courtship involve the male holding his first pair of legs above the female and flicking the tips. Leg flicking occurs less and is generally less vigorous than in males from the AT populations. Leg flicks are coordinated with seismic displays. SR male seismic displays are shorter than AT seismic displays and consist of a single component: a high-intensity, broadband crackle (*a* in Figure 1c). This is similar in frequency content to the AT crackle but is longer in duration (Figure 1c) (Elias et al. forthcoming). SR males include other components similar to AT males (rasp, see above) at extremely short ranges just prior to attempted copulation (Figure 1a, 48–55 s, Santa Rita column). The vast majority of seismic signals produced by individual SR males, including those that produce rasps, only include the crackle component (Figure 1a).

Behavioural trails

Immature females were checked daily to see if they had moulted to maturity. Only virgin adult females aged 16–40 days postmaturation (average 23 days \pm 4.4 SD) were tested in trials, and females were of the same average age for all trial conditions (see below). All male and female spiders were fed 2 days prior to experiments. *Habronattus pugillis* seismic signals are produced by stridulation involving structures on the cephalothorax (prosoma) and abdomen (opisthosoma) similar to other spider species (Legendre 1963; Uetz and Stratton 1982; Maddison and Stratton 1988; Elias et al. 2003, forthcoming). SR and AT males were randomly divided into 2 treatments: (1) muted or (2) nonmuted. Two days prior to the experiments, males were anesthetized with CO₂, and a piece of bee’s wax was placed (1) between the cephalothorax and abdomen (the first and second body regions), ultimately connecting the two and inhibiting their relative movement (muted), or (2) on top of the cephalothorax, but not connecting it to any other body part (nonmuted control). None of the treatments affects visual signals (Elias et al. 2003, 2005), and approximately the same amount of wax was used for both treatments. To ensure that these treatments did not affect normal locomotory activities, we observed whether or not waxed spiders were able to successfully capture prey during the 2 days after these manipulations. SR females were randomly assigned to 1 of 4 treatments: (1) muted, foreign (AT), (2) nonmuted, foreign (AT), (3) muted, local (SR), and (4) nonmuted, local (SR). Trial order was randomized between the 4 treatments. Females and males were each used only once.

A plastic cylinder (12.5 cm in diameter \times 13.5 cm high) was used as the courting arena. A piece of graph paper cut to fit inside the cylinder was used as the arena floor. An opaque

paper ring was placed around the outside of the cylinder to minimize visual distractions. An Electronic Imaging Systems (Rolling Meadows, IL) fiber optic light system was used to illuminate the arena. All trials were videotaped (Canon ZR50 MC, 30 fps) from above. Although some jumping spiders are known to use chemical cues present in female silk for mate location and for initiating courtship (Jackson 1982), *Habronattus* male courtship behavior occurs in the absence of chemical cues, and the initiation of courtship behavior seems predominantly visually based (Elias et al. 2003). In order to prevent the build up of chemical cues, graph paper was replaced every 2 trials and the plastic cylinder cleaned with 95% ethanol at the end of each recording day. Females were placed into the arena first, then males. Only males that courted during a 15-min period were scored, and trials lasted a total of 15 min. We recorded (1) copulation success, (2) male courtship duration (total time male spent courting), (3) latency to copulation (latency from the start of male courtship to copulation), and (4) female attention (time the female’s anterior median (AM) eyes were directly oriented toward a courting male). Copulation success data is reported for males that copulated within 5 min after a female started observing a male’s courtship displays because this is likely to be a realistic measure of mate choice in *H. pugillis* (Hebets and Maddison 2005). Under natural conditions, uninterested females can and will jump away immediately (Hebets and Maddison 2005; DO Elias and EA Hebets, personal observation). Latency to copulation was recorded for males that copulated during the 15-min trial period. Female attention is measured as the time a female spent orientated to a male because jumping spiders are visual specialists and use vision to assess mates, predators, and prey (Forster 1982a, 1982b; Foelix 1996; Harland and Jackson 2002). Jumping spider AM eyes are specialized for high spatial resolution and have a small field of view (Land 1985); hence, it is likely that assessment occurs only if females directly orient their AM eyes toward males.

Copulation proportion data was analyzed using a contingency table analysis with Pearson tests. If this test yielded significant results, pairwise differences between treatments were estimated. Attention and courtship effort were analyzed using analysis of variance (ANOVA) with a Tukey post hoc test with Bonferroni corrections. Statistical tests were conducted using the Systat statistical analysis package (SSI, Richmond, California). Latency to copulation data did not meet the assumptions for normality, hence we performed nonparametric statistics. Nonparametric multiple comparisons were performed using a multiple Behrens–Fisher test (Ullrich and Hothorn 2001). Nonparametric statistics were performed using the R statistical analysis package (GNU, Boston, Massachusetts).

RESULTS

Behavioural trials

There was a significant effect of seismic treatment (muted vs. nonmuted) on male mating success (contingency analysis: $X^2 = 14.481$, $df = 3$, $P = 0.002$). SR females were more likely to mate with nonmuted AT males than muted AT males (contingency analysis: $X^2 = 11.902$, $df = 1$, $P = 0.001$; Figure 2) and muted SR males (contingency analysis: $X^2 = 7.817$, $df = 1$, $P = 0.005$; Figure 2). Although nonsignificant, SR females also tended to mate more with nonmuted AT males than nonmuted SR males (contingency analysis: $X^2 = 13.336$, $df = 1$, $P = 0.068$; Figure 2). No other pairwise differences were observed ($P > 0.05$).

To ensure that our results did not simply reflect differences in male courtship effort, we measured male courtship effort in

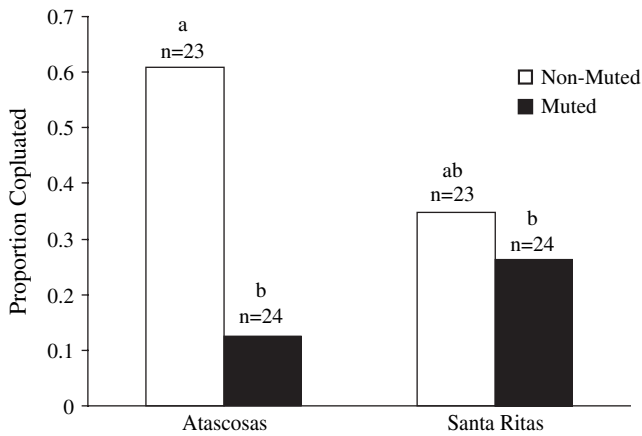


Figure 2
Proportion of males that successfully copulated with females within 5 min. Different letters indicate significant differences ($P < 0.05$). SR females are more likely to mate with foreign AT males only if they can produce seismic signals. SR females do not prefer local SR males that produce seismic signals.

individuals that successfully mated by dividing the latency to copulation by the duration of time that males courted. Males spent the majority of time courting, and no significant differences were observed among any of the treatments (AT nonmuted: 0.96 ± 0.04 , mean \pm SE; AT muted: 0.84 ± 0.12 , mean \pm SE; SR nonmuted: 0.99 ± 0.01 , mean \pm SE; SR muted: 0.90 ± 0.10 , mean \pm SE; $P > 0.05$).

An analysis of female visual attention, measured as total time the female spent looking at the male divided by the total time the male spent courting, showed significant effects of male origin and seismic treatment (male origin: $F_{1,90} = 13.207$, $P < 0.0001$; seismic treatment: $F_{1,90} = 15.172$, $P < 0.0001$; male origin \times seismic treatment: $F_{1,90} = 3.104$, $P > 0.05$). Females paid more visual attention (ANOVA: $F_{3,90} = 10.406$, $P < 0.0001$; Figure 3) to nonmuted AT males than muted AT males (Tukey post hoc; $P = 0.001$; Figure 3), muted SR males (Tukey post hoc; $P < 0.0001$; Figure 3), and non-muted SR males (Tukey post hoc; $P = 0.002$; Figure 3). No other differences were observed between treatments.

SR females mated more quickly with nonmuted AT males than muted AT males (Behrens–Fisher; $P = 0.0184$; Figure 4), nonmuted SR males (Behrens–Fisher; $P < 0.0001$; Figure 4), and muted SR males (Behrens–Fisher; $P = 0.00495$; Figure 4). No other differences were observed between treatments.

DISCUSSION

The xenophilic mating preference previously observed in SR female *H. pugillis* for foreign AT males (Hebets and Maddison 2005) seems to be driven by a female preference for complex and/or novel seismic signals. Although visual displays (motion and ornaments) are dramatically different between populations of *H. pugillis*, the xenophilic preference is sufficiently explained by differences in seismic components of courtship alone; preventing AT males from producing seismic signals eliminates xenophilic preferences. SR females have a higher mating frequency and mate more quickly with seismic signal producing foreign AT males. Interestingly, among local SR males, the presence/absence of seismic signals does not significantly affect mating success. These results suggest that while SR females are using seismic signals from foreign males to make mate choice decisions, they are not using seismic signals from local males. This lack of focus on local male seismic signals may result from an increased importance of

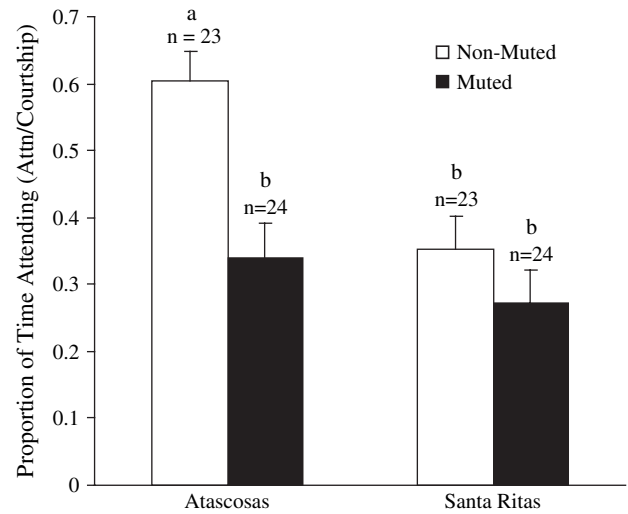


Figure 3
Female attention to male courtship displays. Mean proportion of time (\pm SE) the female spent attending male courtship was calculated by dividing the time the female spent attending male displays by the total amount of time males spent displaying. Different letters indicate significant differences ($P < 0.05$). SR females spend a higher proportion of time attending foreign, AT males only if they produce seismic sounds.

visual signals among local males or alternatively a build up of resistance to local male seismic signals. Because no differences were found in male mating effort between the populations, all observed female mate choice decisions were attributable solely to male courtship traits.

In this system, females appear to prefer males with seismic signals that are more elaborate in form or that contain novel elements, suggesting a bias for seismic signal complexity/novelty. Such female biases have been invoked to explain the origin and evolution of signals in many communication systems, including calling sounds in frogs (Ryan 1990; Ryan and Rand 1990), visual ornaments in swordtail fish (Basolo 1990, 1998), coloration in sticklebacks (Smith et al. 2004), and vibratory displays in water mites (Proctor 1991, 1992).

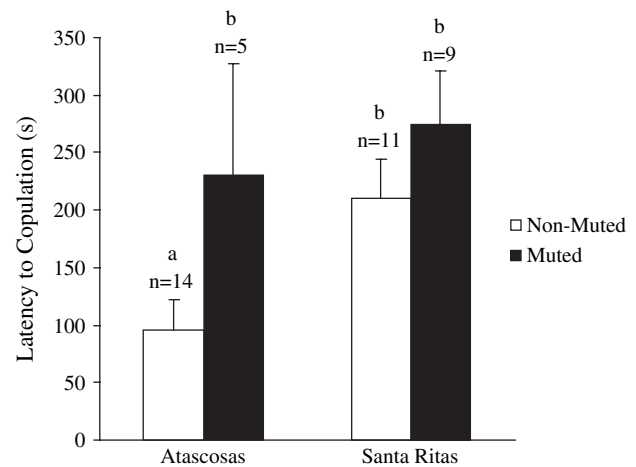


Figure 4
Mean latency to copulation for successfully mated pairs (\pm SE). Different letters indicate significant differences ($P < 0.05$). SR females mate more quickly with foreign, AT males that can produce seismic sounds.

However, in systems where males of some populations have been shown to evolve a particularly attractive trait due to preexisting female biases, females from all populations are expected to be equally predisposed to prefer the attractive trait (Jennions and Petrie 1997). Interestingly, this pattern of female attraction is not found among *H. pugillis* populations as previous work has demonstrated an asymmetric mating preference in which SR females preferred foreign AT males over their own local males, whereas AT females showed no mating preference (Hebets and Maddison 2005). Hebets and Maddison (2005) argued that their results were not consistent with either a pure receiver bias hypothesis or a coevolutionary process of positive reinforcement in which male traits and female preferences were evolving in concert. Instead, they proposed that a process of antagonistic coevolution was consistent with their observed mating pattern and that such a process could be driving the rapid diversification of male courtship displays and associated ornamentation observed among populations of *H. pugillis*. Our results are consistent with this hypothesis.

Under antagonistic coevolution (Holland and Rice 1998), females are expected to evolve resistance to exploitative male signals and to mate only with males that produce “derived” or exaggerated exploitative signals. One prediction from such a process is that females will prefer foreign males with more elaborate forms of traits and/or novel traits over local males for which they have evolved resistance; a prediction that is supported with results from this experiment. Although both populations of *H. pugillis* share a similar seismic component, AT males have a more elaborate seismic display that contains 2 additional components. It is tempting to think of these novel AT seismic components as new armaments in the evolutionary “arms race” between males and females. The further elaboration of exploitative male traits (i.e., seismic components) to overcome thresholds of female resistance is a key prediction in antagonistic coevolution models (“chase-away” selection) that remains to be explicitly tested in this system.

Given our present data, we cannot distinguish among sexual selection processes that may have been, or continue to be, important in the diversification of *H. pugillis* as female biases are important in many processes of sexual selection (Ryan 1990; Ryan and Keddyhector 1992; Andersson 1994; Christy 1995; Chapman et al. 2003). However, results thus far remain consistent with a process involving antagonistic coevolution. For example, Masta and Maddison (2002) observed that some cross-population matings of *H. pugillis* had lower fitness (measured as the number of viable offspring) than within-population matings, suggesting that it may be maladaptive for females to mate with foreign males. In their reciprocal mating trials, Hebets and Maddison (2005) found that 69% of the SR × SR and 45% of the SR × AT crosses resulted in egg sac production (EA Hebets and WP Maddison, unpublished data). Furthermore, they found that 59% of the eggs hatched in SR × SR crosses, whereas only 22% hatched in SR × AT crosses (EA Hebets and WP Maddison, unpublished data), demonstrating a potential fitness cost to SR females of mating with the more attractive foreign AT males. Nonetheless, future work incorporating more population crosses as well as female costs is necessary before we can distinguish between the processes of sexual selection that may be involved in driving the rapid diversification of populations of *H. pugillis*.

The preference of SR females to mate with males producing complex/novel traits appears to be linked with visual attention as SR females pay more attention to AT males only if they produce seismic signals. There are several potential explanations for such a result, yet all remain to be tested. The presence of seismic signals may stimulate a female’s freezing response, ultimately preventing her from escaping. Such

freezing responses can be common in spiders in the presence of predator-related cues or by an “overloading” of a female’s sensory system (Barnes et al. 2002; Persons et al. 2002; Lehmann et al. 2004; Hebets and Papaj 2005). Such an explanation is unlikely however as females actively track male movements while visually attentive. Alternatively, seismic signals may focus a female’s attention on other male traits through cross-modal interactions (Rowe 1999; Candolin 2003; Hebets and Papaj 2005). Such interactions were shown to be important in a wolf spider where seismic vibrations altered a female’s attention to visual stimuli (Hebets 2005).

Habronattus pugillis is an exemplar species within a tremendously diverse genus of jumping spider representing extreme geographic variation in male behavior and associated morphology. The *Habronattus* genus encompasses more than 100 known species in North America and is characterized by an extraordinary diversity and complexity of visual and seismic courtship displays (Peckham GW and Peckham EG 1889, 1890; Griswold 1987; Maddison 1988; Maddison and Stratton 1988; Maddison and Hedin 2003; Elias et al. forthcoming). The diversity observed within and among *Habronattus* species and populations rivals that observed in other taxa with extreme diversifications attributed in part to sexual selection (i.e., haplochromine cichlids—Kocher et al. 1990; Dominey 1994; Seehausen 2000; *Laupala* crickets of Hawaii—Otte 1989; Mendelson et al. 2004). Within *Habronattus*, the observed assortment of male displays incorporates signal diversity within and across multiple sensory modalities with the most diverse species groups possessing the most complex courtship displays (Elias et al. 2005). This pattern, in combination with our results demonstrating a female bias for signal complexity/novelty, suggests that selection due to female preference for greater signal complexity or novelty, rather than selection on particular signal features, could be a strong selective force leading to the rapid evolution and diversification of male-specific characters. Such preferences for signal complexity or novelty may be widespread across animal taxa and may be important in many animal groups with respect to both the origin and maintenance of signal diversity and complexity.

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