

VARIATION OF FEMALE PREFERENCE INFLUENCES THE MAINTENANCE OF PHENOTYPIC DIVERSITY

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Abstract

Female preference is one of the main components of sexual selection that can affect intraspecific phenotypic diversity. In some animal species, the phenotypic landscape of one of the sexes presents a bimodal or multimodal distribution and these phenotypes also differ in their reproductive tactics. Here, I evaluated how female preference influences the coexistence of two male alternative reproductive tactics in the jumping spider *Maevia inclemens*. I employed no-choice tests to analyze variation of female preference between different locations and between the two morphs. Females present a negative-frequency dependent sexual preference choosing the rare morph. Additionally, the female preference functions differ between morphs and these differences can contribute to the maintenance of the discreteness of the traits of the morphs. These results highlight the importance of variation of female preference in the maintenance of alternative reproductive tactics. They also show that negative-frequency dependent selection and diversifying selection contribute to the coexistence of both morphs in the species.

Keywords: female preference, alternative reproductive tactics, sexual communication, diversifying selection, rare phenotype.

INTRODUCTION

Sexual selection can have a significant influence on the maintenance of phenotypic diversity within a species (Gray and McKinnon, 2007). One of the main components of sexual selection is mate choice, exerted more commonly by females (Andersson and Simmons, 2006). Many models have been created to explain how female preference can be the driving force in sexual selection and how it can evolve and be maintained (reviewed in Andersson and Simmons, 2006; Kokko *et al.*, 2006; Jones and Ratterman, 2009). Generally, these models consider female preference as a fixed trait and its variability is included as variance around a mean value.

However, female preference is a complex and elaborate component of sexual selection and it can include substantial variability (Cotton *et al.*, 2006). This variation in female preference can occur at the population level (Endler and Houde, 1995; Boughman, 2001; Simmons *et al.*, 2001; Klappert *et al.*, 2007) as well as among and within individuals in a population (Kodric-Brown and Nicoletto, 2001; Cotton *et al.*, 2006; Parrott *et al.*, 2007). Variation in female preference can have a significant effect on the maintenance of genetic (Rowe and Houle, 1996; Tomkins *et al.*, 2004; Birkhead *et al.*, 2006; Neff and Pitcher, 2009) and phenotypic diversity within a species (Cotton *et al.*, 2006; Gray and McKinnon, 2007). Therefore, this variation must be considered as more than just random deviation from a fixed preference in order to understand its influence on the evolution of the phenotypic landscape of the opposite sex.

In some animals, one sex may exhibit alternative phenotypes that differ in tactics to obtain fertilization or reproduce -called Alternative Reproductive Tactics (ARTs)- (Oliveira *et al.*, 2008). These ARTs can present a bimodal or multimodal distribution and are more commonly found in males than in females (Taborsky and Brockmann, 2010). In some species, male ARTs seem to have originated as a way for males of a particular phenotype to obtain access to females by eluding female preference (Gross,

1991; Shuster and Sassaman, 1997; Watson and Simmons, 2010). Hence, female preference can be an important factor influencing the origin and coexistence of these tactics.

Polymorphism of alternative reproductive tactics simplifies the study of evolutionary dynamics by providing tractable study systems through the division of phenotypic and genetic variation into discrete categories (Cox and Calsbeek, 2011). For most animals, these tactics are bourgeois -individuals that invest in privileged access to females- and parasitic -individuals that exploit the investment of the bourgeois conspecifics- (Taborsky, 1997; Taborsky and Brockmann, 2010). In some taxa, the maintenance of the ARTs is possible due to variation in female preference. Hurtado-Gonzales *et al.* (2010) reported spatial variation in the sexual preference of females of the South American live-bearing fish *Poecilia parae*. In each habitat, females commonly favor one of the several morphs which is selected against by predation in that habitat. This spatial variation in female preference, coupled with predation, allows the coexistence of the different male morphs. In other species, like the pigmy swordtail *Xiphophorus multilineatus*, spatial variation in the strength of female preference allows the coexistence of ARTs (Rios-Cardenas *et al.*, 2007). In this species, populations with weaker female preference for courtiers increased the mating advantage of the alternative tactic, sneakers. Hence, the distribution of variation in female preference within a species can strongly influence the maintenance of ARTs.

Several theoretical models provide explanations for the puzzling coexistence of ARTs (Tomkins and Hazel, 2007). Game theory states that frequency-dependent selection can maintain these different strategies within a single species resulting in mixed Evolutionary Stable Strategies (Maynard Smith, 1982). From this theoretical framework, variability in female preference based on the tactics' ratios could allow the coexistence of several morphs in different locations of the phenotypic landscape of a species. In the guppy *Poecilia reticulata*, negative frequency-dependent female preference can maintain multiple morphs by providing higher mating success to the morph with a frequency lower than the equilibrium frequency (Zajitschek and Brooks, 2008). Additionally, negative frequency-dependence can apply to variation in female preference, causing a feedback cycle that allows the coexistence of the different male phenotypes (Alonzo and Warner, 2000; Kokko *et al.*, 2007).

Furthermore, there must be complementary processes maintaining the character differences between phenotypes. Darwin (1859, 1871) introduced the idea that the mating preferences of one sex can result in selection on the morphological and behavioral traits of the opposite sex. There are different mechanisms through which sexual selection can influence the evolution of sexual and non-sexual characters of the opposite sex (reviewed by Lande and Kirkpatrick, 1988; Miller and Todd, 1995; Andersson and Simmons, 2006). Therefore, variability of female preference will have differential effects on different male morphs, directing them through alternative paths on the phenotypic landscape. To analyze the effect of variation in female preference on the maintenance of alternative reproductive tactics and their discrete traits, it is important to target a system where intersexual selection can have a significant effect in the mating success of the morphs.

Taxa with a large diversity of signals involved in sexual communication evince the influence of sexual selection on the phenotypic traits and reproductive success of the opposite sex (Barraclough *et al.*, 1995; Arnqvist *et al.*, 2000; Seehausen, 2000). Male jumping spiders (Araneae: Salticidae) display a wide variety of vibrant colors (Taylor and McGraw, 2007) and extremely elaborate vision-mediated courtship displays (Clark, 1994; Elias *et al.*, 2012). This is possible because salticids have uniquely elaborate eyes (Land, 1969a, b; Blest *et al.*, 1990) and a spatial acuity surpassing that of many birds and approaching that of primates (Land, 1972; Land, 1974; Williams and McIntyre, 1980; Harland and Jackson, 2000). These characteristics suggest that female preference can act as a selection force on the male traits in this group. Furthermore, Masta and Maddison (2002) reported that spatial variation in female preference in *Habronattus pugillis* (Araneae: Salticidae) resulted in diversifying selection on male sexual traits, causing a divergence in male behavioral and morphological traits between different

populations. Therefore, salticid spiders provide a good study system for addressing questions related to sexual selection and female preference in particular.

I focused on one species from the Eastern and Midwestern United States, *Maevia inclemens* (Araneae: Salticidae). This species presents two male ARTs, since it has two distinctive genetically determined male morphs, the Grey (G) morph and the Tufted (T) morph (Clark, 1992). The phenotypes have very similar anatomical characteristics early during development, but when they reach sexual maturity they differ considerably in their coloration pattern and initial courtship phase (Fig. 1; Clark, 1992). The G morph has striped legs, yellow pedipalps and orange spotting of the abdomen. Its courtship consists of crouching down and pointing its first and second pairs of legs forward (adopting the shape of an arrow) while gliding sideways in receding semi-circles in front of the female. On the other hand, the T morph has a completely black body, with white legs and three tufts above the anterior median eyes. During the initial courtship phase, it stands up by stretching the last three pairs of legs and points the first pair upwards while it waves them vigorously by extending and bending them. Meanwhile it also waves its pedipalps up and down and swings the abdomen, which points downwards, in a semi-circular pattern. Hence, in contrast to many other species with ARTs, in *M. inclemens* both morphs invest in access to copulation by employing different courting tactics (Hoefler, 2008). Consequently, there is no parasitic tactic and female preference can act on both phenotypes, providing an excellent opportunity to analyze the role of female preference in the maintenance of ARTs and as a diversifying force. As it is often the case in evolutionary biology, studying the exceptions to a rule can provide unique insights into more general explanations.

Here I investigate how female preference influences the mating success of the male morphs in *M. inclemens*. Based on game theory, I hypothesize that females modify their preference based on the morphs' ratio in their environment. If *M. inclemens* presents a negative frequency-dependent female preference, then I expect to find that females prefer the morph encountered at a frequency lower than the equilibrium frequency in the population. Additionally, as males in this jumping spider present two discrete morphs that differ in coloration and courtship displays, I tested if female preference promotes the divergence of the morphs' phenotypic traits. If females can differentially influence the phenotypic traits of the morphs, then I expect to find that female preference functions - which quantify preference strength relative to variation in male traits or signals- differ between morphs granting greater copulation success to males with traits differing from the alternative morph.

MATERIALS AND METHODS

Study species: courtship, copulation and sired offspring

The male courtship presents two different phases described by Clark (1994) and the morphs differ only in the initial phase. Both morphs employ very similar signals in the second phase, which consists in the male's approach towards the female. In cases where males successfully copulated, females would display receptivity signals (Clark, 1994) or remain stationary (Crane, 1949; Forster, 1982), allowing the male to approach them. When the male mounted the female, she adopted a particular posture arching her body dorsally and stretching their legs sideways. After insemination was over, females would throw the males sideways and run away from him. In events that ended in no copulation, females would not allow the males to approach by running away. They would not allow males to mount them or they would shake them off immediately after being mounted. I also observed a female cannibalizing the male when he tried to mount her (data point excluded from all the analyses). This female control over the copulation events is possible because females weigh significantly more (♀ Weight = 33.67 ± 1.13 mg; ♂ Weight = 13.04 ± 0.26 mg; $t = 15.412$, $df = 132$, $p < 0.001$) and are significantly larger than males (♀ Length = 8.15 ± 0.09 mm; ♂ Length = 5.87 ± 0.04 mm; $t = 21.248$, $df =$

132, $p < 0.001$). These observations suggest that females directly control copulation in the species because males seem to require female consent to copulate.

Clark (1992) reported that females that mated with only one male, had male offspring that favor the paternal morph. The average ratio of sired sons that resemble the paternal morph was 63%, compared to 37% that resembled the other morph (i.e. 1.7:1). A genetic model with one autosomal and one sex-linked gene was constructed explaining this bias. Because of this genetic determination of the morphs, female sexual preference influences the morph ratio of the offspring.

Collection of specimens and surveying morph frequencies

I collected specimens ($n = 214$) in different natural areas surrounding the city of Ann Arbor MI, United States from May to June, 2012 (corresponding to the reproductive season). Individuals were collected from four different locations: Edwin S. George Reserve (ESGR), Mary Beth Doyle Park (MBD), Maybury State Park and Olson Park (Supplementary Fig. 1). Within these locations, I captured the individuals in similar environments to avoid a bias due to environmental conditions. I collected them at the ecotone between forest and grassland, where the Northern Swamp Dogwood (*Cornus racemosa*) was present, because they were more abundant in areas where this plant was found (*personal observation*). Both males and females were collected from all locations using sweep netting (Clark, 1992) for the calculation of sex ratio, abundance and frequencies of male morphs.

Maintenance of specimens

All specimens collected during field surveys were housed individually in acrylic boxes (10 cm x 10 cm x 20 cm). I provided each individual with water in cotton stoppered vials and fed them twice a week with a mix of *Drosophila* species (*D. melanogaster*, *D. virilis*, *D. americana* and *D. novamexicana*). I enriched the environment of the spiders by adding twigs and leaves to the cages, which is important to avoid alteration of the spiders' behaviors (Carducci and Jakob, 2000). The individuals were visually isolated from each other by cardboard separators placed between boxes, to avoid influence on the morph ratio they perceived in their environment. Spiders were maintained in a growth chamber on a 14:10 h light:dark cycle at 25 °C. Individuals were checked daily to monitor molting and determine when they reached sexual maturity.

Female Preference and Courtship Characteristics

I analyzed female preference using no-choice tests (Hebets, 2003). The tests were carried out during the reproductive season, from May to June. I used only mature virgin females that had not oviposited eggs before the trial ($n = 44$). I considered as virgin the females that had molted to maturity after I collected them, since females can only be inseminated after reaching maturity (when their epigynum becomes fully developed). Females from the different locations were randomly assigned to one male of either morph and from any location.

Prior to each trial, I weighed individuals of both sexes on an electronic scale (SI-124, Denver Instruments). To measure dimensional characters, I photographed them dorsally and ventrally over a millimeter paper sheet with a digital camera (Sony HX1). I measured the width of the prosoma and body length from the dorsal and ventral photographs employing Photoshop CS6 (Adobe). For each individual, I also calculated the Body Condition Index (BCI) from the residuals of the regression between the log transformed mass and the width of the prosoma (Jakob *et al.*, 1996).

The No-Choice tests were carried out in circular arenas to provide a homogenous spatial environment for the encounters. The arenas were built with two stacked cardboard cylinders of 203.2

mm diameter. I placed a millimeter paper sheet between the cylinders to provide a suspended substrate for the transmission of the vibrations, which are an important component of the male courtship (Elias *et al.*, 2010). This sheet also allowed me to measure detection distances. The cylinders provided a uniform contact with the substrate, avoiding a bias in its surface tension due to unequal support of the paper sheet. The inner wall of the cylinder was covered with petroleum jelly to prevent the individuals from escaping from the arena. Additionally, I placed a foam ring between each cylinder and the millimeter paper sheet to avoid the transmission of external vibrations that could be picked up by the cylinders. The arena was also placed over a foam sheet to isolate from possible vibrations of the bench. Since *M. inclemens* detects light in the UV region (Peaslee and Wilson, 1989), I illuminated the arena with a bulb that emitted light in the visual and UV spectrum (26 W Repti Glo 5.0).

For each trial, I placed a new millimeter paper sheet as the substrate of the arena and I also wiped the walls of the arena with ethanol to remove any residues and avoid the influence of silk and pheromones from previous encounters. I placed a female in the arena and allowed 20 minutes of acclimation. Afterwards, I placed a randomly selected male into the arena. Because preliminary work on this species showed that 20 minutes was sufficient time to allow copulation to take place (data not shown), the encounters lasted until copulation finished or 20 minutes had elapsed, whichever happened first. I defined copulation as the insemination of both of the female's spermathecae and insemination as the insertion of the embolus into one of the spermathecae. When the introduction of the embolus was successful, the male would vigorously shake the posterior leg of the opposite side from the pedipalp employed.

To facilitate the scoring of the behavioral variables, the encounters were recorded employing two video cameras (Sony HDR-CX160). One was fixed on top of the arena and the other one was held by hand. The latter allowed me to zoom in and focus on the male behaviors from the most suitable angle, providing a larger and clearer image of the behaviors. I would zoom in the event and choose a proper angle to obtain at least a 500 x 500 pixel image of the individual's full body in lateral view.

To evaluate female preference, I scored the presence/absence of copulation (Clark and Biesiadecki, 2002). I also documented the copulation latency: time elapsed since females first saw the courtship until copulation started (Fig. 2). This variable is a measure of female preference, as it includes the time since females perceived not only the male but also its intentions to copulate. Hence, the latency reflects the preference of the female for the male that has already signaled its sexual intentions and it is inversely related to the preference of the female (i.e. short latency suggests stronger preference). Another variable I scored was copulation difficulty: mounting time needed for the insemination of both spermathecae. Insemination itself was very quick, lasting from 1 to 5 seconds, and the copulation duration extends only when females make it harder for males to perform inseminations by vigorously shaking or running to throw off the male. Hence, as females control the duration of the copulation, copulation difficulty is another variable representing female choice. Females that show a strong preference for the male will allow both inseminations to occur faster, reducing the time until the end of the copulation. These variables allowed me to determine if there is differential preference for each morph and how it varies between the different populations.

I also analyzed the differences in female preference for anatomical (weight, length, prosoma width and BCI) and behavioral traits of each morph (Fig. 2). To determine male behavioral traits that could influence female preference, I scored from each encounter detection latency (time elapsed until male detected the female), detection distance, courtship latency (time elapsed since male detected the female until it began courting), mean courtship time and total courtship time (because males usually courted more than once).

Statistical Analyses

For these analyses I only employed the ESGR and Olson populations' data due to the larger number of individuals collected at these locations, reducing the possibility of sampling bias. I evaluated if the sex and male morph ratios of each population differed from 1:1 employing χ^2 Goodness-of-fit tests. I also analyzed the differences in the copulation probabilities between morphs, locations and between the observed and predicted copulation probabilities employing χ^2 tests. I employed a GLM analysis to test for differences in female preference in the quantitative variables (latency to copulation and copulation difficulty). I also employed a GLM to examine if male anatomical and behavioral traits differed between morphs and between female locations, to make sure that all females were exposed to similar males. A third GLM was employed to analyze the female preference for the male traits.

I employed a χ^2 Goodness-of-fit test to examine if the copulation probabilities of the morphs differed between populations. This test was a more appropriate option than the GLM analysis because the latter does not have enough power for the analysis of the binomial response variable with a small sample size. For this analysis, I considered the data from one population as the observed value and the expected value was calculated based on the copulation probabilities from the other population. If there were no influence of the environment on female preference, then I would expect non-significant differences between populations. I also employed a χ^2 test of independence to analyze if the copulation probability of each morph differed for females from the same location. Furthermore, to provide stronger support, I also employed another χ^2 Goodness-of-fit to compare the observed copulation probabilities to the probabilities predicted by game theory based on the natural morph ratios observed in each population. Since the probability of copulation with the G morph was very close to 0.5 for both populations, it was taken as its expected probability. The expected probability for the T morph in each population was the product of the probability of the G morph multiplied by the G/T ratio of that population. This multiplication modified the probability of the T morph inversely to its frequency in that population, as expected if there was negative-frequency dependent female preference.

For the GLM analyses of the copulation latency and copulation difficulty, the model employed was:

$$Y_{ij} = \beta_0 + \beta_1(\text{FemaleLocation}_i) + \beta_2(\text{Morph}_j) + \beta_3(\text{FemaleLocation}_i)(\text{Morph}_j) + \varepsilon_{ij}$$

where Y_{ij} : response variable (copulation latency or copulation difficulty), β_0 : general mean, β_1 : effect of the female location on the preference, β_2 : effect of the morph on the preference, β_3 : interaction between female location and morph and ε_{ij} : error. If the female preference function varies between populations, then the interaction would show a significant effect.

I employed the same model to analyze if there were differences in the male anatomical and behavioral traits between the different morphs and female location. In this case the response variables were the different anatomical (weight, length, prosoma width and BCI) and behavioral male traits (detection distance, detection latency, courtship latency, mean courtship time, total courtship time). For both GLM analyses the link function was an Identity function for Normal distribution.

For analysis of the female preference for the male traits of each morph I employed a GLM with copulation as the binomial response variable. The model employed was:

$$\text{Ln}\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 X_{1i} + \beta_2(\text{Morph}_j) + \beta_3 X_{1i} \cdot (\text{Morph}_j) + \varepsilon_{ij}$$

where p : probability of copulation = 0, β_0 : general mean, β_1 : effect of the continuous male variable X_1 on the preference, β_2 : effect of the morph on the preference, β_3 : interaction between continuous variable X_1 and morph and ε_{ij} : error. If females prefer the same traits on both morphs, then β_1 should show a

significant effect. If female preference function varies between morphs, then the interaction should be significant.

RESULTS

Sex and Morph Ratios

The sex ratio of the populations was not significantly different than one (ESGR $\delta/\text{♀} = 0.95$, $n = 84$, $X^2 = 0.048$, $p = 0.827$; Olson $\delta/\text{♀} = 1.09$, $n = 92$, $X^2 = 0.174$, $p = 0.677$), supporting the idea that sampling was uniform in the different locations. However, the male morph ratios varied between populations (Fig. 3). The locations with larger sample sizes showed different morph ratios. The ESGR population's morph ratio was similar to 1:1 ($G/T = 1.17$, $n = 41$, $X^2 = 0.243$, $p = 0.622$) while the Olson's ratio was significantly different from 1:1 ($G/T = 1.82$, $n = 55$, $X^2 = 4.083$, $p = 0.043$).

Female Preference

Female preference varied depending on the population from which the females were collected. The copulation probability functions showed significant differences between the ESGR and Olson populations (Fig. 4; $X^2 = 4.295$, $p = 0.038$). Females collected at the ESGR preferred both morphs equally ($X^2 = 0.004$, $p = 0.94937$). However, females from Olson showed a marginally significant preference for the T morph ($X^2 = 3.405$, $p = 0.065$). Additionally, female preference did not differ significantly from the expected copulation probabilities based on the negative frequency-dependent female preference hypothesis, ESGR ($X^2 = 0.360$, $p = 0.549$) and Olson ($X^2 = 0.108$, $p = 0.74$), when calculated from the observed morph ratio from their respective populations. Hence, the observed copulation probabilities did not differ from those expected if females prefer the rare morph.

Females also differed among populations in their latency to copulation (Fig. 4); as there was a significant interaction between female location and morph (Likelihood Ratio $X^2 = 10.771$, $df = 4$, $p = 0.029$). Females from ESGR showed a shorter latency period for the G morph, while females from Olson copulated quickly with the T morph. Additionally, I found the same significant interaction between female location and morph for copulation difficulty (Fig. 4; Likelihood Ratio $X^2 = 11.414$, $df = 4$, $p = 0.036$). Females from ESGR demonstrated shorter times for the G males, while females from Olson had shorter times for the T males. Therefore, these two variables also show variation in female preference between populations.

Preference for male phenotypic characters

Measurements of anatomical variables of the males that were presented to the females did not differ significantly between morphs, female locations nor the interaction between these two variables (Table 1). The behavioral variables did not show any significant differences either (Table 1), except for courtship latency for which Olson females experienced longer latencies than females from ESGR (Wald $X^2 = 8.299$, $df = 1$, $p = 0.004$). Nevertheless, this increment in courtship latency in both morphs for Olson females was proportional to the morphs' latencies observed for ESGR. Hence, the relative differences between morphs were kept constant between females from different locations. The lack of differences in all the other variables showed that females from the different locations encountered males with similar characteristics.

On the other hand, I did observe a significant effect of some of these variables in the copulation probabilities. Within the anatomical variables, the width of the prosoma significantly affected the copulation success (Table 2; Wald $X^2 = 4.362$, $df = 1$, $p = 0.038$). Females preferred males with a wider

prosoma. Additionally, the copulation outcome was significantly influenced by the interaction between weight and morph (Fig. 5; Wald $X^2= 6.574$, $df = 1$, $p = 0.010$) and the interaction between BCI and morph (Fig. 5; Wald $X^2= 6.125$, $df = 1$, $p = 0.013$). Regarding the behavioral variables, three variables showed a significant interaction with the morph: detection latency (Fig. 6; Wald $X^2= 4.442$, $df = 1$, $p = 0.035$), courtship latency (Fig. 6; Wald $X^2= 5.882$, $df = 1$, $p = 0.015$) and mean courtship time (Fig. 6; Wald $X^2= 6.861$, $df = 1$, $p = 0.009$). None of the other anatomical and behavioral variables nor their interactions with the morph had any significant effect on the copulation probabilities (Table 2).

DISCUSSION

Female preference in jumping spiders varied depending on the population of origin and demonstrated a strong bias favoring the rare morph. This finding suggests a possible mechanism of negative frequency-dependent selection acting on the maintenance of the morphs in nature. For each morph, females also expressed different preference functions for several anatomical and behavioral characters. These differences could be contributing to the maintenance of the discrete anatomical and behavioral trait differences between morphs.

Female-biased sexual size dimorphism has been shown to increase the influence of pre-copulatory female preference on male mating success in spiders and insects (Roggenbuck *et al.*, 2011; Puniamoorthy *et al.*, 2012). In *M. inclemens*, females are heavier and larger; therefore, it is likely that they can influence male mating success by exerting control over the copulation events. Males have to court females to obtain a successful copulation. Hence, the courtship displays of the different males are important in the encounters with a female. Since both morphs present clear differences in traits related to sexual communication (coloration and courtship), females can evaluate each morph differently as potential mates. This differential evaluation contributes to the idea that female preference can have a strong impact on the maintenance of the morphs in nature.

Females from different locations showed differential preferences towards distinct male morphs. Females from Olson preferred T morph males while females from ESGR showed either no preference or preferred the G morph. This pattern was observed in all the variables for female preference scored in this study (copulation probability, copulation latency and copulation difficulty). Since in ESGR the morph ratio was close to one and in the Olson population the T morph was at a lower frequency, the three variables suggest that there could be a negative frequency-dependent female preference maintaining the morphs in nature. Nevertheless, the copulation probability is the most informative variable, because it ultimately controls the occurrence of insemination. The similarity between the G/T morph ratio in the Olson population (ratio = 1.82) and the T/G copulation probability ratio (ratio = 1.76) would also provide support for the existence of negative frequency-dependent female preference. This mechanism could allow the maintenance of both morphs in the environment and would help to balance the frequencies if disturbed by other natural factors. This situation has also been observed for the maintenance of polymorphism in the guppy *P. reticulata* (Zajitschek and Brooks, 2008) and in several species of *Drosophila* (Sisodia, 2000). Furthermore, mathematical models of negative frequency-dependent female preference support the idea that the mechanism allows the coexistence of distinct male phenotypes (Alonzo and Warner, 2000; Kokko *et al.*, 2007).

For females to express preference for a particular morph based on the morph ratio, they probably need to obtain this information by sampling their habitat. In *Schizocosa uetzi* (Araneae: Lycosidea), the experience of females as subadults influences their preference when they reach sexual maturity (Hebets, 2003). Hence, in *M. inclemens* females could be assessing the morph ratio before they reach maturity. This appraisal is possible in a system with protandry (i.e. males maturing earlier than females), a common trait in spiders (Gunnarsson and Johnsson, 1990; Maklakov *et al.*, 2004). Protandry was observed in *M. inclemens* since mature male morphs were collected along with subadult females.

Therefore, females would have been able to gather information regarding the morph ratio in their habitat before reaching sexual maturity. A bias based on differential habitat of the morphs is unlikely since males of both morphs were collected in the same habitat and even in the same sweep. Additionally, Clark (1992) found no differences in habitat selection between morphs. Hence, females are likely to have an accurate estimate of the morph ratio in their environment before reaching sexual maturity. Furthermore, there must be some fitness advantages for this mechanism to originate in the first place and be maintained through time.

There are several possible factors that could favor a negative frequency-dependent female preference in the jumping spider *M. inclemens*. Since the morphs are genetically determined (Clark, 1992), one factor could be increased genetic diversity of the offspring and decreased inbreeding, which has been showed to cause severe depression in fitness (Saccheri *et al.*, 1996; Bilde *et al.*, 2007). Another factor may be avoidance of a decrease in clutch size, since it has been shown that individuals born from genetically dissimilar parents tend to have larger than average number of offspring (Amos *et al.*, 2001). Since the morphs are genetically determined, if a particular morph is more abundant, then we can infer that the majority of the females were sired by that morph as well because the offspring sex ratio is 1:1 (Clark, 1992). Hence, females would benefit from choosing males of the opposite morph, increasing the genetic diversity of their offspring. This benefit would hold even when the genetic distance between morphs is not large, because the probabilities of mating with a non-related male would increase. Another possibility is that frequency-dependent female preference would reduce the predation probabilities for the offspring. Predators selectively focus their attention on recently and commonly encountered prey types while ignoring the alternatives (Bond and Kamil, 1999, 2002). This search-image formation has also been seen in jumping spiders that are possible predators of *M. inclemens* (Jackson and Li, 2004). Hence, females could increase the chances of survival of their offspring by mating with the less frequent morph. Additionally, dividing the male population into two morphs would decrease the probabilities that predators would form search-images of them. It is also advantageous to present dimorphism in males rather than in females, since males are the most active sex (Clark, 1992), which would make them more easily detectable. These factors are not mutually exclusive and all of them would benefit female preference for the rare morph.

Even though evidence points towards a mechanism of negative frequency-dependent female preference, there are other factors that could influence female preference, such as relatedness of individuals (Tregenza and Wedell, 2000; Mack *et al.*, 2002; Stow and Sunnucks, 2004; Archie *et al.*, 2007; Hoffman *et al.*, 2007) and their familiarity (Clarke and Faulkes, 1999; Hughes *et al.*, 1999; Gerlach and Lysiak, 2006; O'Connor and Shine, 2006). However, to minimize the influence of these factors, the females were exposed to random males from several different locations that were from 10 km up to 45 km apart. Another possible explanation is that female preference could exhibit fixed probabilities for selecting the different morphs, allowing the coexistence of the different phenotypes in particular frequencies (Partridge, 1988). However, in this scenario the preferred morph should be more abundant, which was not observed. There could be an ecological selection force, such as predation, acting against the preferred morph, as was observed in the South American live-bearing fish *P. parae* (Hurtado-Gonzales *et al.*, 2010). This study does not allow me to rule out the existence of a complementary ecological factor acting against the T morph in the Olson population, causing its numbers to decrease. However, it would still suggest the existence of a negative frequency-dependent female preference since females would prefer the rare morph. Regardless of which mechanism is operating in the populations, female preference appears to be influencing morph mating success.

It is also interesting to note that out of the 114 males collected, none belonged to an intermediate nor mosaic morph. Furthermore, there are no reports of intermediate phenotypes from previous work on the species (Painter, 1913; Clark, 1992). This discrete phenotypic distribution suggests the existence of a force maintaining the discrete differences between the morphs. In this study, I found

that for the anatomical (weight and BCI) and behavioral traits (detection latency, courtship latency and courtship duration) females showed different preference functions for each morph. They prefer heavier T morph males and with a higher BCI and G males with lower BCI, while they are indifferent to the weight of the G males. Regarding the behavioral traits, females show consistency in their preference, preferring shorter times for the behaviors of the G males while longer times for the T males. They prefer G males with shorter detection latencies, courtship latencies and mean courtship times while they were indifferent to the detection latencies in the T males but do prefer in them longer courtship latencies and longer mean courtship times. The fact that the morphs did not show significant differences in any of these traits was due to large variation within morph. And this could be because the average ratio of sired sons that resemble the paternal morph is 63%, compared to 37% that resemble the other morph (Clark, 1992). The mixed offspring would allow an increase in variability within morph since a fraction of one morph is sired by males of the opposite morph. However, the differences in the female preference functions for each morph could contribute to maintaining the discreteness of the male morphs in the species. A divergence on the male traits because of variable female preference was also observed in *H. pugillis* (Masta and Maddison, 2002), supporting the idea that female preference can act as a mechanism for the diversification of mating and sexual related traits within a species. Furthermore, it has been suggested that phenotypic divergence in species with ARTs could be the starting point of speciation (Corl *et al.*, 2010).

These processes that act entirely within a species are of particular interest because they could contribute to the evolution of reproductive isolation and sympatric speciation by sexual selection, a controversial topic in evolutionary biology (van Doorn *et al.*, 2004; Gavrillets and Hayashi, 2005). Sexual selection is generally assumed to play a direct role on the diversification of sexual and mating related traits (Andersson, 1994; Eberhard, 2010) and is considered an important diversifying process (Gavrillets, 2000; Panhuis *et al.*, 2001). Furthermore, variation in female preference can also act as a diversifying selection force (Boughman, 2001; Boughman, 2002; Seehausen *et al.*, 2008). In many studies, it has been observed that there is a correlation between species richness and traits involved in sexual communication or sexual selection, suggesting the role of sexual selection in speciation (Barracough *et al.*, 1995; Owens *et al.*, 1999; Arnqvist *et al.*, 2000; Seehausen, 2000; Mank, 2007). With over 5000 species, Salticidae is the largest family in Araneae (Platnick, 2012). Additionally, jumping spiders have acute eyesight (Land, 1972; Land, 1974; Williams and McIntyre, 1980; Harland and Jackson, 2000), and males present vibrant coloration (Taylor and McGraw, 2007) and elaborate courtship displays (Clark, 1994; Elias *et al.*, 2012). Because of these characteristics, female preference could be an important diversifying selection force in this taxon. Consequently, the high species number in Salticidae could have resulted from different speciation events driven by sexual selection. It would be very interesting to analyze the role of variation in female preference on the diversification processes in Salticidae.

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