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Repeatable female preferences, mating order and mating success in the poeciliid fish, *Heterandria formosa*

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Abstract Sexual selection via female choice can afford preferred males comparably higher mating success than those males that lack preferred traits. In addition, many models of sexual selection assume that both male traits and female preferences are heritable. In this study we test whether females of the poeciliid fish, *Heterandria formosa*, have repeatable pre-copulatory preferences for larger males. We also test whether female pre-copulatory preferences are always reliable indicators of male mating success. When given a choice between a large and a small male, females prefer larger males, and the repeatability of this preference is high. Although there are no overall differences in male mating success between large and small males, large males have a higher mating success when they are the first to mate than when they are the second to mate. Likewise, preferred males also have higher mating success when they are the first to mate than when they mate second. Therefore, the repeatable female preferences observed in this study only predict male mating success when the preferred male mates first. These results illustrate that even significantly repeatable female preferences do not translate into male mating success, which is an assumption of many examinations of the importance of female choice in sexual selection.

Keywords Mating costs · Poeciliidae · Repeatability · Sexual selection

Introduction

There is a general acceptance in behavioral ecology that females are able to detect differences in conspecific male traits and base mating preferences on those differences (review in Bradbury and Andersson 1987; Andersson

1994). Sexual selection via female pre-copulatory choice is expected to increase the mating success of males possessing a preferred trait relative to males without the trait. However, this form of intersexual selection can be countered by other sources of selection such that males with preferred traits do not necessarily have a higher net mating success. Intersexual selection has been investigated in a number of species (review in Andersson 1994), and in many taxa, females exhibit pre-copulatory preferences for larger males (Brown 1981; Hughes and Hughes 1985; Ryan and Wagner 1987; Simmons 1987; Hastings 1988; Poole 1989; Basolo 1998b). It is often assumed in such studies that pre-copulatory preferences are positively correlated with male reproductive success. For example, studies of lekking ungulates indicate that females may be safer from harassment by conspecific males or from predation on leks, and therefore prefer to associate with and mate with males on leks to solitary males (Deutsch and Weeks 1992; Clutton-Brock et al. 1993).

Lack of a positive correlation between female pre-copulatory preferences and male mating success may suggest several, non-mutually exclusive processes. First, direct male–male competition may override female pre-copulatory mate choice (Andersson 1994). Second, the evolution of alternative male reproductive strategies, such as sneaky copulations, may override female pre-copulatory choice (Dunbar 1982; Henson and Warner 1997). Third, female pre-copulatory choice that is subverted by intrasexual selection may lead to the evolution of post-copulatory control of fertilization.

Intersexual selection has been investigated in a number of poeciliid fish species (Endler 1983; Ryan and Wagner 1987; Farr 1989; Reynolds and Gross 1992; Basolo 1995, 1998a; Houde 1997). These fishes exhibit internal fertilization, and females give birth to live young. Males possess a gonopodium, which is modified from the anal fin, and is used to transfer spermatophores to the female gonopore. Females are often larger than males. Numerous studies have demonstrated a female preference for larger poeciliid males (Ryan and Wagner

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1987; Morris et al. 1996; Basolo 1998b; Ptacek and Travis 1998). The pre-copulatory behavior of male poeciliids involves varying degrees of courtship display, with males of some species appearing to exhibit little or no courtship behavior. In other species, males have an apparent conditional strategy that allows them to either court females or attempt sneak copulations (review in Farr 1989). Sneaky copulations are effected via gonopodial thrusting, which has been hypothesized to circumvent pre-copulatory female acceptance of males (Rosen and Tucker 1961; Farr 1989). Sneak gonopodial thrusting occurs when a male swims from behind, under, or to the side of a female with the gonopodium forward, and attempts to bring the tip of the gonopodium near to, or in contact with, the female gonopore in an attempt to copulate (Farr 1989). An alternative to this is when a male exhibits courtship within a female's field of vision and then swims along her flank and ejects a sperm packet near her gonopore.

One poeciliid with considerable sexual size dimorphism is *Heterandria formosa*. This poeciliid is native and abundant in swamps and ditches from Florida northward to the Carolinas, and westward to southern Louisiana. Males in this species are small, and the gonopodium is 35–40% of the male standard length (personal observation; Bisazza and Pilastro 1997). Farr (1989) concluded that male *H. formosa* rely mainly on gonopodial thrusting rather than courtship for mating. Bisazza and Pilastro (1997) report that small male *H. formosa* can have a mating advantage over large males, when they employ gonopodial thrusting because male copulatory success, measured as the number of successful gonopodial thrusts, was negatively correlated with male standard length. In *H. formosa* better maneuverability could explain the mating advantage of small males. In addition, if not detected by the female lateral line system, females may not notice smaller males when they approach the female from the 'blind' portion of the female's visual field (Bisazza and Pilastro 1997), and thus female choice could be subverted.

In this study, we examine female preferences and male mating success in *H. formosa* by addressing three main questions. First we ask, do females demonstrate pre-copulatory mating preferences for larger males, and are individual female preferences repeatable? This question addresses the consistency of female preferences. In order to determine if female preferences are consistent, they must be measured more than once, and estimates of the repeatability must be determined. Repeatability sets the upper limit of heritability. Heritability of preferences is an assumption of most models of female choice (Boake 1989). Second, we consider how female mating preferences, male body size, and male mating order affect male mating success. Lastly, we consider how female mating preferences, male body size, and male mating order affect female behavior.

Methods

The fish used in this experiment were progeny of wild-caught fish collected in November 1997 in Orleans Parish, LA. The fish were maintained in the laboratory on a 16 h:8 h photoperiod, and were fed twice daily, brine shrimp in the morning, and TetraMin flakes in the afternoon. Prior to sexual maturation, the fish were housed in communal tanks. All test fish were raised in individual tanks after reaching sexual maturity.

Forty-two males were measured for standard length (SL: measured from the snout to the caudal peduncle) to the closest mm. A total of 14 pairs of males that differed in SL were matched for the female preference tests. Standard length difference (SL large male–SL small male) ranged from 0.4 to 2.3 mm (mean \pm SE: 1.221 ± 0.563). All test females were virgins, which ensures that the females possessed a high degree of mating receptivity.

Female preference and repeatability:

The female preference tests were conducted in a tank similar to that used with other poeciliid species (Houde 1997). The 18.9 l tank measured 40.6×20.3×25.4 cm and was divided into three equal sized compartments. The center compartment was further divided into three sections, each measuring 4.5 cm. The two end compartments were separated from the center compartment by two 0.32-cm-thick glass dividers consisting of a sheet of polarizing filter between two glass panes. The two polarizing filters were aligned to prevent fish in the side compartments from observing one another, but allowed the test female in the center of the tank to see the fish in both side compartments. The compartment dividers were sealed to the tank with silicone to eliminate effects of chemical cues. The tank was surrounded on three sides with black plastic and was placed in a soundproof chamber. The uncovered side of the tank faced a pane of one-way glass. For each test trial, the interactions of the test fish were observed from the other side of the one-way glass. Trials were conducted from 0800 to 1000 hours. During tests the tank was illuminated with a full spectrum of light.

We used a method common to poeciliid fishes to investigate female choice (Ryan and Wagner 1987; Stoner and Breden 1988; Basolo 1990b, 1995; Houde and Torio 1992; Kodric-Brown 1992). Each trial consisted of two 10-min observation periods. At the beginning of each trial a female was placed in the center compartment. Two removable opaque dividers visibly blocked the two side compartments. One male of a pair was placed in one side compartment, and the other male was placed in the other side compartment. The fish were allowed to acclimate for 10 min, after which time the opaque dividers were removed. Each trial was scored for the amount of time the female spent in each of the three sections of the center compartment (left side, center, right side), and the amount of time the female spent in close proximity (within 2 female SL) to a male exhibiting behavior described in the literature for poeciliids indicative of courtship [e.g., glides, body curves, forward and backward swim (Farr 1989)]. This was our measure of female mating preference. After the first 10-min trial, the opaque dividers were replaced and the two male sides were switched to control for side biases. Following another 10-min acclimation period, the second 10-min trial commenced, and the amount of time a female spent next to a male exhibiting mating behavior was once again recorded. The data from both trials were summed for a total test time of 20 min per female. Following this test, all fish were returned to their home tanks. The following day, the same three test fish were used in a second, identical preference test.

We estimated the repeatability of female preferences across the 2 days of preference tests. Repeatability was calculated from the mean square (MS) among groups (females) and the MS between groups (error) from a one-way ANOVA on the average time (across both days of testing) each female interacted with the larger male–average time each female interacted with smaller male (Lessels and Boag 1987). The standard error associated with this

measure of repeatability was calculated as the square root of the sampling variance of the intraclass correlation (Becker 1984). We also examined whether females preferred larger males by comparing the average amount of time a female spent with the larger male versus the average amount of time a female spent with the smaller male using a paired *t*-test.

Male mating success and female behavior

Immediately following the second preference test, one of the males was chosen randomly, removed from the test tank, and returned to his home tank. The remaining male was then placed in the center compartment with the female, and the fish were allowed to interact for 12 h. The two fish were videotaped for a total of 345 min throughout the 12 h. The 345 min of videotaping consisted of the first 180 min of the trial, with the remaining time videotaped for 15 min every hour thereafter, until the end of the mating trial. Following this 12-h period, both fish were returned to their home tanks. The following day the same female and the other male of the pair were placed in the center compartment of the test tank and videotaped, as the day before. The videotapes were scored for: (1) number of copulation attempts (number of gonopodial forward rotations positioning the gonopodium near the female gonopore); and (2) copulation success (number of gonopodial forward rotations that resulted in contact between the male gonopodium and female gonopore). The tapes were also scored for the number of times a female approached a male and made contact with the male's body with her mouth. This behavior is described in the literature for some poeciliids as a nip, and has been suggested to be either a behavior involved in courtship or a behavior involved in aggression (Schlosberg et al. 1949).

Mating success was operationally defined as the number of successful copulations divided by the number of attempted copulations, which controls for the effects of differential male activity. Using paired *t*-tests, the independent effects of body size, preference status, and mating order on male mating success were compared between: (1) preferred and non-preferred males; (2) large and small males; and (3) the first male to have female access and the second male to have female access. To further examine male mating success, we analyzed: (1) the effect of mating order and male body size on the mating success of preferred and non-preferred males; (2) the effect of mating order and preference status on the mating success of large and small males; and (3) the effect of male body size and preference status on the mating success of the first male to mate and the second male to mate. Each of the preceding analyses utilized two-way ANOVA.

Using paired *t*-tests, we determined if females directed nips differentially between: (1) larger and smaller males; (2) preferred and non-preferred males; and (3) first male to have access to the female and second male to have access to the female. We also determined if male copulation success was significantly correlated with female nipping behavior.

Results

Female preference and repeatability

There was considerable variation in the preference scores of individual females for large males, which ranged from 80s to 660 s (out of a total of 1,200 s of testing per day; Fig. 1). Individual females differed from one another in their preference for large males (ANOVA: $F_{13,14}=6.20$, $P=0.0009$; see Table 1). Therefore, although females tend to spend more time with larger males, the strength of this preference varies between females. The repeatability of preference scores between days was high, and significantly greater than 0 ($r=0.722\pm 0.133$).

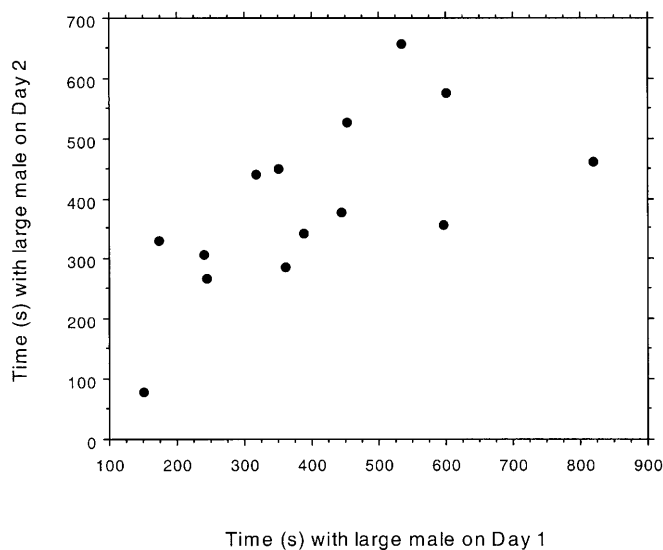


Fig. 1 Relationship between the amount of time individual females ($n=14$) spent with larger males in trials repeated on successive days

Based on the average time females spent exhibiting mating behavior towards males across the 2 days of testing we found that female *H. formosa* spent significantly more time with the larger males (mean \pm SE: 397.5 ± 150.3 s) than with the smaller males (mean \pm SE: 208.1 ± 109.2 s) (paired *t*-test: $t_{13} = 2.865$, $P=0.013$).

Male mating success and female behavior

Preference status

Overall, there were no differences in male mating success between preferred and non-preferred males (Table 1). However, preferred males did have greater success at mating when they were the first to have access to the female than when they were the second (Tables 2, 3a). There was no difference in mating success between large preferred males and small preferred males (Table 2). There were no effects of mating order or of male body size on mating success of non-preferred males (Tables 2, 3a).

Male body size

Overall, there was no difference in male mating success between large males and small males (Table 1). However, large males had higher mating success when they were the first to have access to the female than when they were the second (Tables 2, 3b). There was no difference in mating success between large preferred males and large non-preferred males (Tables 2, 3b). There were no effects of mating order or of preference status on mating success of small males, yet there was a significant interaction between these variables (Tables 2, 3b).

Table 1 Means \pm SE and results of paired *t*-tests on male mating success and female nips directed at males. *n*=14 for each test

	Male mating success \pm SE		Female nips \pm SE	
Preferred male	0.215 \pm 0.042		36.143 \pm 5.013	
Non-preferred male	0.201 \pm 0.039 <i>t</i> =0.221	<i>P</i> =0.829	16.714 \pm 4.906 <i>t</i> =2.664	<i>P</i> =0.020
Large male	0.220 \pm 0.165		28.286 \pm 5.413	
Small male	0.197 \pm 0.037 <i>t</i> =0.371	<i>P</i> =0.717	24.571 \pm 5.821 <i>t</i> =0.412	<i>P</i> =0.687
First male	0.258 \pm 0.038		28.500 \pm 5.561	
Second male	0.159 \pm 0.038 <i>t</i> =1.802	<i>P</i> =0.095	24.357 \pm 5.669 <i>t</i> =0.461	<i>P</i> =0.653

Table 2 Mean male mating success by male size, male preference status, and male mating order

Size	Preference status	Mating order	Mating success (SE)
Large	Preferred	First	0.330 (0.065)
Large	Preferred	Second	0.102 (0.052)
Large	Non-preferred	First	0.335 (0.045)
Large	Non-preferred	Second	0.125 (0.125)
Small	Preferred	First	0.330 (0.001)
Small	Preferred	Second	0.095 (0.015)
Small	Non-preferred	First	0.126 (0.044)
Small	Non-preferred	Second	0.254 (0.074)

Mating order

Overall, there was no difference in male mating success between the first and the second male to mate (Table 1). Furthermore, there were no effects of male body size or of preference status on mating success of the first male

Table 3 Results of two-way ANOVAs on (untransformed) male mating success. *Order* Male mating order; *size* male body size, *status* male preference status (based on the average time female spent with male across 2 days of female preference tests). Significant *P*-values are italicized

Variable	Factor	<i>df</i>	MS	<i>F</i>	<i>P</i>
a Preferred male mating success	Order	1	0.153	10.900	0.008
	Size	1	0.000	0.002	0.961
	Order \times Size	1	0.000	0.002	0.961
	Error	10	0.014		
Non-preferred male mating success	Order	1	0.005	0.262	0.620
	Size	1	0.005	0.250	0.628
	Order \times Size	1	0.082	4.456	0.061
	Error	10	0.018		
b Large male mating success	Order	1	0.136	7.649	0.02
	Status	1	0.000	0.025	0.879
	Order \times Status	1	0.000	0.021	0.887
	Error	10	0.018		
Small male mating success	Order	1	0.008	0.551	0.475
	Status	1	0.001	0.093	0.767
	Order \times Status	1	0.094	6.346	0.030
	Error	10	0.015		
c First male mating success	Size	1	0.036	3.120	0.107
	Status	1	0.033	2.869	0.121
	Size \times Status	1	0.045	3.923	0.076
	Error	10	0.012		
Second male mating success	Size	1	0.009	0.392	0.545
	Status	1	0.002	0.088	0.773
	Size \times Status	1	0.010	0.427	0.528
	Error	10	0.023		

to mate, or on mating success of the second male to mate (Tables 2, 3c).

Female behavior

Female nipping behavior did not differ with male body size (Table 1). Although females did not direct more nips towards the first male to mate, females did direct significantly more nips towards preferred males than towards non-preferred males (Table 1). In addition, male mating success was significantly correlated with the number of nips directed at males ($r=0.378$; $P=0.04$) (Fig. 2).

Discussion

Female preference and repeatability

Our study demonstrates a pre-copulatory preference by female *H. formosa* for larger males compared to smaller

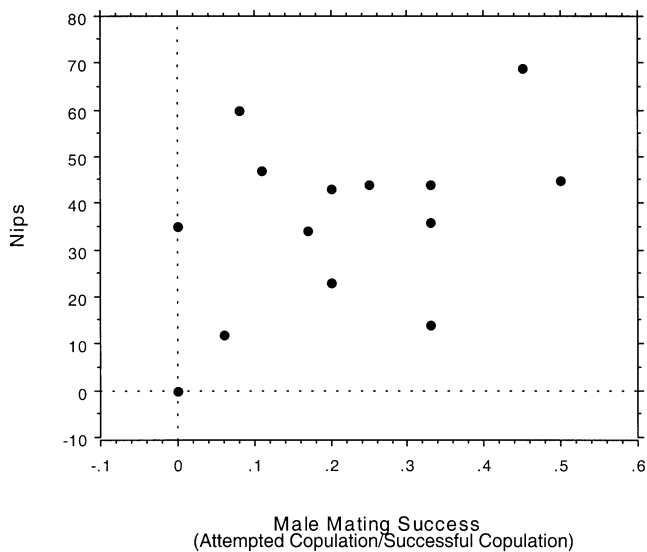


Fig. 2 Relationship between male mating success ($n=14$) and the number of nips received by each male from females

males. This preference may be based on body size per se, a character correlated with body size, or both. There are a number of different sexual selection models that explain why females may prefer a given trait in males, including: direct benefits (Trivers 1972; Halliday 1978); good genes (Williams 1966; Hamilton and Zuk 1982); Fisherian processes (Fisher 1930; Kirkpatrick 1982); correlated effects (Lande 1980; Halliday and Arnold 1987; Basolo 1996); and pre-existing receiver biases (West-Eberhard 1984; Endler and McLellan 1988; Basolo 1990a, b). These models assume (except for some cases of direct benefits) that both female preferences and the male traits have a heritable component. Any one or a combination of these models could explain the preference in female *H. formosa* for larger males.

In this study, we found high repeatability of female preference. Individual females are therefore consistent in their pre-mating behavior over time. Assessing heritability in female preferences is a difficult task, but estimates of repeatability set an upper limit to heritability (Boake 1989). As a result, there is consistent variation between females in the strength of their preferences. Repeatability of female pre-mating preferences has been demonstrated in several studies (Møller 1994; Godin and Dugatkin 1995; Wagner et al. 1995; Brooks 1996; Johnsen and Zuk 1996), and has been found to range from low to high. In addition to providing an upper limit to heritability, repeatability may be an indicator that the methods used to detect female preferences are valid, consistent measures.

Male mating success

Summing male mating success for the first and second day of mating, we found that male mating success was not predicted by female preferences. There were no dif-

ferences in mating success between large and small males, or between preferred and non-preferred males. There are at least three explanations for these results. First, there may be countering sexual selection in the form of male–male competition. In poeciliids, direct male–male competition may play a more important role in male mating success than pre-copulatory female preference, as implied by the small male mating advantage reported by Bisazza and Pilastro (1997). Although males in our experiment did not have the opportunity for direct contact, the effects of male–male competition in the evolutionary history of this species may have shaped behaviors currently exhibited by males, such as sneaky copulations by small male fish. Second, there may be alternative reproductive behaviors in males that override selection via female choice. For example in frogs (*Hyla* spp.), in the presence of a female preference for large size, when there are multiple male mating strategies, there may be no differential mating success of the males (Wells 1977; Perrill et al. 1978; Forester and Czarowsky 1985; Ryan and Keddy-Hector 1992). In our study, thrusting behavior of male *H. formosa* may not only be an alternative to direct male–male competition, it may also reflect past selection on males to counter the effects of female choice. *H. formosa* field sites in Louisiana experience temporal and spatial heterogeneity, resulting in periods of open waterways, or periods of isolated pools (personal observation). During this time, when *H. formosa* may be densely packed in isolated pools, thrusting behavior may be particularly effective in circumventing female choice.

A final possibility for the lack of a relationship between female preference and male mating success is that the experimental methodology does not accurately measure female preferences. It has been suggested that the amount of time a female spends in close proximity to males does not always reflect female preferences (Gabor 1999). This assertion is based on the idea that females may associate with larger individuals as a result of natural selection arising from predation pressure. This, however, is one of the bases of the pre-existing receiver biases model for the evolution of mating preferences (Basolo 1990b; Endler and Basolo 1998). That is, any female behavior that results in some males having greater access to females and thereby experiencing a mating advantage over other males is sexual selection. Thus, if males in close proximity to females are more likely to mate with females than males who are not, female association time is a valid measure of sexual selection via female mate choice. Additionally, by positioning herself in close proximity to a large preferred male, a female may avoid unwanted copulations from smaller, non-preferred males because larger males are likely to deter small male mating attempts. Thus remaining near a preferred male may improve the chances that female preferences are not subverted. In *H. bimaculata* it appears that when given the choice to be near one of two males, or either a conspecific juvenile or female, test females spend significantly more time with each male than with the other conspecific

ics, and they spend significantly more time with one class of males versus the other class of males to which they are presented (Basolo, in press). If our measure of female preferences was simply a result of schooling behavior or an anti-predation strategy, then test females should not spend more time with other males than with conspecifics.

We found that although large males do not have a higher mating success than small males, they do have higher mating success when they are the first to have access to a female than when they are the second. This same effect is found with preferred males. This result is not surprising given that, overall, females prefer larger males. There are at least two explanations for why a preferred male has high mating success only when he mates first. One of these explanations concerns the cost of mating (Daly 1978). Once females mate with a preferred male, they may resist further matings from subsequent males because of potential costs of mating. Important costs of mating in our system may include: sexually transmitted disease (Rosenqvist and Johansson 1995); physical damage during transfer of sperm (Hildemann and Wagner 1954; Lewis and Pollock 1975); toxins present in seminal fluids (Chapman et al. 1995); increased risk of predation (Wing 1988); or reduced foraging time.

Our results concerning male mating success are not consistent with those reported by Bisazza and Pilastro (1997). Both studies measured male mating success as the number of successful copulation attempts divided by the total number of copulation attempts, in order to correct for any differences in male activity. We examined the possibility that non-preferred males may have attempted more copulations than preferred males to have the same number of successes, which could skew the estimate of mating success. In our study, non-preferred males did not attempt more copulations than preferred males (mean \pm SE attempts by non-preferred male = 13.43 \pm 3.73; mean \pm SE attempts by preferred male = 15.79 \pm 2.37; paired *t*-test: *t*=0.59; *P*=0.566). One significant difference between the two studies is that we used only offspring of wild-caught fish, and only virgin females, whereas in Bisazza and Pilastro (1997), the receptivity of females was unknown, and fish were obtained from fish dealers. Furthermore, we had a much longer time period in which we observed male mating success (345 min compared to 60 min), and Bisazza and Pilastro (1997) were not consistent in the amount of time during which they scored mating behavior. Finally, in our experiment, females were first presented with the two males, and then the males were presented to females sequentially. In the previous study, the females were not given an opportunity to make a choice between males. Prior exposure to the males by females may have significantly affected the mating success of males.

Female nipping behavior

In addition to the effects of mating order on male mating success, there is also a significant correlation between

male mating success and the number of nips a female directs at the male during the mating trial. Furthermore, females direct more nips at preferred males than to non-preferred males. Schlosberg et al. (1949) identify nips as a behavior preceding mating, when performed by green swordtails and platyfish males, and suggest it stimulates females. Males alternate this behavior with other pre-mating behavior such as arching and fin contact to the females' ventral area. However, Schlosberg et al. (1949) also suggest that the nips of a female could indicate aggressive behavior. Our results suggest that nips may best be described as a female mating behavior as opposed to a female aggressive behavior. Females may use nips on males as a signal that they are willing to mate, or to assess male chemical cues.

Conclusion

Overall, this study demonstrates two main points. First, female preferences for large body size in male *H. formosa* are likely to have some heritable component, given our measure of repeatability, and can therefore have ramifications for sexual selection in this species. Second, female preferences do not always predict male mating success. Many studies of female choice have assumed that a significant female preference for a trait will translate into male reproductive success. Here we have measured male mating success (which is likely a closer measure of male reproductive success), and demonstrated that a significant and repeatable female preference does not predict a male's mating success. One reason evident in our study is that mating order can have significant effects on the outcome of male-female interactions. This effect needs more attention in future studies of how female preferences may affect male reproductive success. Our study provides an examination of the dynamic interactions of mating order, female mating preference, as well as body size on male mating success.

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