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# State-Dependent Mate-Assessment and Mate-Selection Behavior in Female Threespine Sticklebacks (*Gasterosteus aculeatus*, Gasterosteiformes: Gasterosteidae)

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## Abstract

Most investigations of mate-choice have focused on the outcomes of mate-choice (i.e. which mates are chosen), and thus we generally know very little about how mates are chosen (i.e. how mates are found, assessed, and selected). Mate-choice by females has been shown to be dependent on the state of the female, with females being less selective when limited by time or energy. This result could be caused by changes in female mate-assessment or mate-selection behavior. We examined whether manipulations of time and energy affected the mate-choice behavior of female threespine stickleback (*Gasterosteus aculeatus*). We found that female mate-choice behavior, when not divided into stages, was affected by both of the manipulations. This matches previous findings. When we divided female courtship behavior into six stages, we found that the two manipulations affected different portions of the mate-choice process. The holding-time manipulation changed female behavior at the beginning and end of the mate-choice process and the swimming manipulation changed female behavior only at the end of the mate-choice process. Neither of the manipulations significantly affected female behavior in the middle portion of the mate-choice process. Thus, the mate-choice process appears to be composed of multiple state-dependent decisions. We discuss how a better mechanistic understanding of how female state affects female mate-choice behavior can produce testable predictions and provide a basis for investigating the evolution of mating systems.

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## Introduction

Making informed choices between options, be they alternative mates, habitats, or food items, can be a complicated process involving multiple tasks, such as identifying options, assessing the options, and selecting an option. Unfortunately, because few mate-choice studies have focused on exactly *how* individuals choose mates (Gibson & Langen 1996; Jennions & Petrie 1997), we know very little about how these tasks are achieved and to what degree they are integrated.

Mate-choice and its effects on sexual selection and mating systems are best understood by studying how females choose mates through the mate-assessment process and the mate-selection process. (We use 'mate-selection' to refer to a female's decision to mate with a male and 'mate-choice' to refer to the process that includes finding, assessing, and selecting a mate). For example, several studies have shown female mate-choice behavior to vary with the female's state or the state of her environment, where higher sampling costs (i.e. decreased energy reserves, decreased time, higher predation risk, or larger traveling costs) lead to less selective mate-choice (Bakker & Milinski 1991; Milinski & Bakker 1992; Forsgren 1992; Hedrick & Dill 1993; Godin & Briggs 1996; Backwell & Passmore 1996; Gotthard et al. 1999). However, less selective mate-choice could result from several mechanisms. For example, females could be less thorough in assessing their options before choosing a mate or could lower their standards when selecting a mate. Changes in mate-assessment and mate-selection decisions can only be distinguished by observing female behavior during the whole mate-choice process and noting how it is altered by their state.

Both theoretical and empirical evidence suggest that mate-assessment and mate-selection decisions may differ in their functions and should be viewed separately (Gibson 1996). Mate-choice models, for instance, show that distinguishing between mate-assessment and selection may be critical for understanding behavior. Luttbeg (1996) presents a mate-choice model that, unlike alternative models, allows females to choose which males they visit and assess. The model predicts that, in addition to a male's estimated quality, female decisions to assess a male are influenced by the costs of assessment, familiarity with a male, and the clarity of a male's signal. For example, when a female visits or courts a male, it may be because he is unfamiliar or inexpensive to assess, and not because she estimates him to have high quality. Such results from theoretical studies show the importance of distinguishing mate-assessment from mate-selection.

Recent empirical studies also demonstrate the importance of incorporating the assessment process into studies of mate-choice, as well as distinguishing between mate-assessment and selection decisions. In particular, the process of

choosing a mate can be composed of multiple steps, and the decisions and traits associated with those steps are obscured if the mate-choice process is analyzed as a single step (Backwell & Passmore 1996; Gibson 1996). Gibson (1996) found that one male sage grouse (*Centrocercus urophasianus*) trait, inter-pop interval, affects whether female sage grouse visit a male, but has no effect on female mate-choice once the visit has begun. Conversely, another male trait, display rate, does not affect whether a female visits a male, but does affect whether the female mates with the male during the visit. Previous studies that did not isolate the decisions to visit and to mate failed to detect the effect of display rates, because inter-pop interval and display rate co-vary inversely, and mixing the decisions masked the effects of the two traits. Backwell & Passmore (1996) found that male claw size affects whether female fiddler crabs (*Uca annulipes*) visit a male, but has no effect on whether a female mates during a visit. However, the characteristics of a male's burrow, which are unlikely to be known to the female when the visit begins, do affect whether a female mates. A study solely using correlations between male mating success and male traits would fail to recognize the proximate mechanisms of how female fiddler crabs assess and choose their mates.

Studying the process of mate-choice requires continuous observations and experimental protocols that allow courtship to progress relatively unhindered. Because most mate-choice studies focus on determining what male traits affect inter-sexual selection, they use protocols that prevent males and females from freely interacting (partitions: Dugatkin & Godin 1992; Milinski & Bakker 1992; Godin & Briggs 1996; video and audio playbacks: Gerhardt 1987; Ryan & Rand 1990; Hedrick & Dill 1993; Rowland et al. 1995). These protocols typically use female proximity to a male or female behaviors directed towards a male to indicate that a female has chosen a mate. However, because courtship is not allowed to progress naturally, it is not possible to interpret how male traits or female state affect the steps of the mate-choice process. Our view is that the process leading to selecting a mate can only be fully understood if courtship is allowed to follow its normal course, with sequential events being recorded continuously (see Wittenberger 1983). This will usually require that females have free access to multiple males, which will introduce complicating factors such as male–male competition and male mate-choice.

The threespine stickleback (*Gasterosteus aculeatus*) is well suited for the study of the mate-choice process. It has long been a classic research subject for mate-choice and sexual selection studies (Tinbergen 1951), yet it is also a species in which mate-choice is protracted and potentially complicated in the field (Foster 1994, 1995). Females appear to choose the males they assess and the males they select as mates. When females have ovulated (releasing eggs into the lumen of the ovary) and are competent to spawn (Wootton 1974), they leave foraging groups and move individually among territories held by reproductive males, sequentially courting males before selecting a mate (Foster 1994, 1995). Although males often initiate courtship, females can (and often do) control who they assess by controlling how far a courtship proceeds and by rejecting the initiation of courtship. In addition, females can control the extent to which they assess
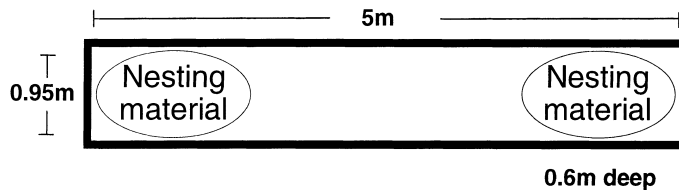
potential mates by courting with males multiple times (Luttbeg 1997). The pattern of their courtship behavior is fairly consistent and has been divided into defined steps (Goldschmidt & Bakker 1990). These steps serve as a good basis for studying parts of the mate-choice process.

Female sticklebacks are known to adjust their mate-choice behavior to changes in their state, at least under conditions in which interactions between females and males are restricted. In the study of Bakker and Milinski (1991), the general female preference for males with bright nuptial coloration became less strongly expressed as the time past ovulation increased. In the study of Milinski and Bakker (1992), females that swam against a current or were held for longer spent more time near drably colored males than did control females. However, because the protocols prevented unencumbered interactions between males and females, it was not possible to separate the mate-choice process into steps and ask which steps caused the observed changes in female interactions with drably colored males.

In this study, we examine the processes of mate-assessment and selection by female threespine sticklebacks. We take advantage of these previous studies (Bakker & Milinski 1991; Milinski & Bakker 1992) by repeating some aspects of their design to show the importance of taking an expanded view of the mate-choice process. Specifically, we investigate how two manipulations, one of female time and the other of female energy, affect steps in the courting behavior of female threespine sticklebacks. We find, as in previous studies, that the two manipulations affect female mate-choice behavior, but we also find that the two manipulations affect different portions of the mate-choice process.

## Methods

Threespine sticklebacks were caught in Big Lake (61°32′ N, 149°48′ W) in the Matanuska–Susitna Valley of Alaska. The fish were housed and experiments were conducted at the Big Lake Hatchery in Big Lake, Alaska. Males were caught with minnow traps and dip nets. They were grouped into pairs based on size (≤ 1 mm difference in standard length) and released into experimental arenas (Fig. 1). Gravid females were caught with minnow traps that were emptied and



Fig. 1: The experimental arenas were four concrete salmon runs. At the two ends of the arenas, nesting material and sand were provided and a wire cage (30 × 30 cm bottom) containing a gravid female was suspended partially in the water to induce male nesting. These gravid females were not used in experiments

reset each morning. We judged females to be gravid by the distention of their abdomen and the dilation of their cloacae. Females captured on the same day were held as cohorts and housed outdoors in plastic pools. The fish were fed daily with live plankton and frozen brine shrimp.

### The Manipulations and Experimental Design

Six pairs of males were used in the experiment. On three successive days, each pair of males was sequentially presented two females. Female state was manipulated according to a $3 \times 2$ design in which the two factors were holding-time and swimming.

The first factor, holding-time, was intended to vary the amount of time which females had available for assessing and selecting a mate. Gravid females can only hold their eggs for a few days before either having to dump them or risking becoming egg bound (Wootton 1976; Guderley 1994). Holding-time was the number of days we held gravid females before using them in an experiment (0, 1 or 2 d). Because we did not know how long females had been gravid before we caught them, there is variance within our holding-time categories for this variable. However, because females typically spawn soon after becoming gravid (Wootton 1974), the scale of our manipulation of holding-time should introduce substantial variance in the length of time for which females had been gravid. The presentation order of holding-times was systematically varied across pairs of males.

The second factor, swimming, was intended to manipulate female energy reserves. Swimming against a current is energetically demanding (Lester 1971), particularly for gravid females (Wootton 1976). Reducing the energetic states of females should make spending remaining energy to assess and select mates more costly than it is for females with unmanipulated energy reserves. One member of each female pair (the swim female) was forced to swim against a current. The current, approximately 10 cm/s, was established in the ring channel of a 2.30-m diameter wading pool with a 1.8-m diameter wading pool in its center. A pump (60 Hz, 1.7 A) placed in the ring produced the current. Within the channel, the female was held in a wire box (57 cm long, 16 cm wide, and 37 cm deep), where she swam against the current for 20 min. To encourage the experimental female to swim, we placed three larger females from a different lake into the wire box with the subject female. The second female in the pair (the control female) was placed in the box for 20 min with the same three large females but no current. The order of control vs. swim presentation was reversed each day for each pair of males.

Each day we conducted two mate-choice trials using a pair of gravid females held for the same number of days. After experiencing the swimming manipulation (either swim or control), a female was moved to the experimental arena in a cup. She was released into the middle section of the arena (Fig. 1) by dipping the cup into the water and waiting for her to swim out. One hour after the first trial ended, a second female, with the other swimming manipulation (swim or control), was similarly released into the experimental arena.

## Trials and Observations

During trials, two people made continuous focal observations of the female. One observer, the primary observer, described the behavior of the female and males (Fig. 1). The other observer transcribed the behavior of the female and males onto data sheets and aided in observations.

Trials could end three ways: (i) the trial was ended after 1 h if the female never initiated courtship and rejected all attempts by males to initiate courtship; (ii) the trial was ended after 2 h if the female initiated courtship or responded positively to males that initiated courtship during the first hour; (iii) the trial was ended at the time a female entered a nest, in which case the female was forced out of the nest before she could spawn and was removed from the arena. This procedure never damaged a nest and no males abandoned their nests.

We tested whether nest entry was a good indication of mate-selection. In the final trial for a pair of males, and in other experiments, we did not disturb females that entered a nest and we observed whether spawning followed a female's first entry into a nest. Nest entry appears to be a good indication of mate-selection, with 19 out of 23 females (82.6%) spawning in the first nest they entered.

## Courtship Behavior

When analyzing courtship activity, we divided courtship into steps based on the classification of Goldschmidt & Bakker (1990), and scored every courtship for its furthest step reached. The steps (defined below) were: 1, courtship initiated; 2, female shows interest; 3, female follows the male; 4, female follows the male to his nest; 5, female places her snout into the nest entrance; and 6, female enters the nest. Wootton (1976) and Rowland (1994) describe the steps of courtship behavior. Courtship reached step one either when the female swam to a male, placing herself above him and against his dorsal spines, or when a male initiated courtship by moving towards the female, either directly or in a zig-zag dance. A courtship bout ended when the female turned away from the male (unless she was in a head-up posture), or when courtship activity ceased for 2 min. Courtship reached step two if the female responded positively to male courting by turning towards the male or by exhibiting a head-up posture. Courtship reached step three if the pair dorsal pricked (the pair rises up and backwards with the female above the male and against his dorsal spines), meandered (the pair swim in slow circles with the female above and slightly behind the male), or if the female followed the male toward his nest. Courtship reached step four if the female followed the male to within approximately 10 cm of the nest entrance, and it reached step five if the female placed her snout in the male's nest as he showed her the entrance. Finally, courtship was scored as reaching step six if the female entered the nest completely.

We combined the female's interactions with the two males and calculated the probability of transitions between each successive step of courtship. For example, the transition probability $p_{12}$ for a female was calculated by dividing the number of courtship sequences in which the female showed interest in courting (step two)

by the number of courtship sequences that were initiated by either male or by the female (step one). We combined female interactions with either male because our focus is on the behavior of the female and pseudo-replication occurs when each female produces two sets of transition probabilities. In addition, some females interacted with only one male, thus separate transition probabilities for both males would weight trials differently. The transition probabilities are conditional, so their existence depends on females achieving the starting condition. Thus, sample sizes for transitions later in the courtship sequence can be smaller. Otherwise, the transition probabilities are free to vary independently.

### Statistical Analyses

ANOVA's were used to test for significant effects of the holding-time manipulation, classified on an ordinal scale, and the swimming manipulation, classified on a nominal scale, on transition probabilities. For ease of interpretation and because only two out of six possible interaction terms were significant, we report the results without the interaction terms included, unless otherwise stated. Prior to the ANOVA, we performed an arcsine transformation on each transition probability using Freeman and Tukey's modification (Zar 1984). Following the ANOVA, we calculated the power of detecting a significant effect of either manipulation on each transition probability using G*Power (Buchner et al. 1997). A significance level of 0.05 was assumed, as was a 'large' effect size (f = 0.4, with f being the standard deviation of the treatment means divided by within-treatment population standard deviation; Cohen 1988; Winer et al. 1991).

### Results

We first tested whether the swimming and holding-time manipulations affected how mate-choice trials ended. Females were more likely to enter a nest when they were held for more days (zero out of 12 females held for 0 d, six out of 12 females held for 1 d, nine out of 12 females held for 2 d entered a nest, $\chi^2$-test: $\chi^2_2 = 18.77$, p < 0.01). The swimming manipulation did not significantly affect how mate-choice trials ended (six out of 18 control females, and nine out of 18 swim females entered a nest, $\chi^2$-test: $\chi^2_2 = 1.03$, p = 0.31).

We next tested whether the two manipulations affected how quickly females chose a mate. For trials in which a female entered a nest, the swimming manipulation significantly affected the amount of time that expired from the beginning of the mate-choice trial to nest entry, but the holding-time manipulation had no significant effect (ANOVA: swimming p < 0.05, time expired: swim females 1349 ± 621 s, control females 3613 ± 462 s; holding-time p = 0.97, no day 0 females entered a nest, day 1 females 2090 ± 689 s, day 2 females 2499 ± 771 s).

We find that extensive variability in female mate-choice behavior is overlooked when the effects of manipulations are judged on the outcomes of trials or the speed of female mate-choice decisions. For example, the number of

*Table 1:* Number of times (mean and range) females reached the various stages of courtship. A courtship sequence scored as reaching a courtship stage may have reached further stages as well. Experimental design prevented females from entering a nest more than once

| Number of times reached | All females | | Females that entered a nest | |
|---|---|---|---|---|
| | Mean ± SE | Range | Mean ± SE | Range |
| 1. Courtship initiation | 52.1 ± 8.4 | 1–210 | 28.6 ± 8.1 | 1–109 |
| 2. Female shows interest | 25.3 ± 5.5 | 0–117 | 17.9 ± 5.4 | 1–69 |
| 3. Female follows male | 21.8 ± 5.1 | 0–116 | 15.8 ± 4.6 | 1–56 |
| 4. Female follows male to nest | 11.4 ± 3.6 | 0–92 | 6.0 ± 1.8 | 1–25 |
| 5. Female inserts snout in nest | 7.6 ± 2.6 | 0–81 | 4.5 ± 1.3 | 1–20 |
| 6. Female enters nest | 0.4 ± 0.1 | 0–1 | 1 ± 0 | 1 |

courtship sequences in which females participated ranged from zero to 117 (Table 1). Among females that ultimately entered a nest, the number of courtship sequences that they participated in during a trial ranged from one to 69 and the number of times they inserted their snout into a nest ranged from one to 20. Three females entered a male's nest during their first courtship. In contrast, five females had in excess of 25 courtship sequences before they entered a nest. At every stage of courtship, some females rejected males, as shown by the declining average occurrence of each subsequent stage (Table 1). In particular, females often rejected males after placing their snouts into a male's nest. Therefore, threespine stickleback courtship appears to be composed of a series of female decisions to continue courting or reject the male.

The probability that a courtship initiation (defined as either the male swimming towards the female directly or in a zig-zag pattern, or the female swimming directly to the male) led to a female entering a male's nest, $p_{16}$, incorporates more of the variability in female mate-choice behavior than the outcome or speed of mate-choice trials. Without the interaction term, both manipulations significantly affected $p_{16}$ (Table 2), with females that were held for more days or were forced to swim against a current before their mate-choice trial being more likely to go from courtship initiation to entering a nest than females held briefly or control females. In this case, the interaction of the two manipulations did significantly affect $p_{16}$. The nature of the interaction was that the swimming manipulation appears to affect $p_{16}$ for females held for 1 or 2 d, but not females held for 0 d (Fig. 2a).

Because both manipulations affected female mate-choice behavior when viewed as a whole, we examined how the two manipulations affected each of the transitions between the six stages of courtship. The first transition, $p_{12}$, was significantly higher for females that were held captive for more days (Fig. 2b and Table 2). The swimming manipulation did not significantly affect $p_{12}$ and the power of this test was moderate (0.64). The second transition, $p_{23}$, was not

*Table 2:* Results of ANOVAs of the two manipulations vs. transition probabilities (without interaction terms)

| | Swimming manipulation | | | Holding-time manipulation | | |
|---|---|---|---|---|---|---|
| | f Ratio | p | power | f Ratio | p | power |
| $P_{16}$ | 8.56 | < 0.01 | 0.64 | 3.94 | < 0.05 | 0.52 |
| $P_{12}$ | 1.85 | 0.18 | 0.64 | 3.44 | < 0.05 | 0.52 |
| $P_{23}$ | 0.01 | 0.94 | 0.57 | 0.18 | 0.83 | 0.45 |
| $P_{34}$ | 3.18 | 0.09 | 0.56 | 1.28 | 0.30 | 0.44 |
| $P_{45}$ | 6.00 | < 0.05 | 0.49 | 2.95 | 0.07 | 0.38 |
| $P_{56}$ | 7.62 | < 0.05 | 0.48 | 5.86 | < 0.01 | 0.36 |

significantly affected by either of the manipulations and the powers of these tests were also moderate (Table 2). The interaction of the manipulations significantly affected $p_{23}$, with the swimming manipulation having opposite effects on females held for 1 d vs. females held for 0 or 2 d (Fig. 2c). In addition, $p_{23}$ tended to be near 1.0, which means that when females showed interest in a male they typically then followed him. This suggests that showing interest and following a male may not be separate decisions for female threespine sticklebacks. For the third transition, $p_{34}$, neither manipulation had a significant effect (Fig. 2d and Table 2), but the effect of the swimming manipulation was marginally significant (the power of these tests tended to be weak). The fourth transition, $p_{45}$, was significantly higher for females that swam against a current than for control females and was marginally higher for females held for more days; the test was statistically weak (Fig. 2e and Table 2). The final transition, $p_{56}$, was significantly affected by both manipulations (Fig. 2f and Table 2), with females held for longer and females that swam against a current being more likely to enter a nest than females held briefly or control females.

In summary, both manipulations affected $p_{16}$ similarly, with $p_{16}$ being significantly lower when females were held for more days or when they swam against a current before their mate-choice trial. However, the two manipulations affected transitions between stages of courtship differently. Only the holding-time manipulation significantly affected $p_{12}$. While both manipulations significantly affected $p_{56}$, only the swimming manipulation significantly affected $p_{45}$.

## Discussion

We believe that for many species the process of choosing a mate can be viewed as a sequence of steps, and mate-choice behavior can be quantified as the probability of transitions between these steps. Using this approach we examined how manipulations of time and energy affected the mate-choice behavior of female threespine sticklebacks. When we analyzed the mate-choice process as a single step, we found that females which swam against a current or were held captive for more days were more likely than controls to proceed from courtship
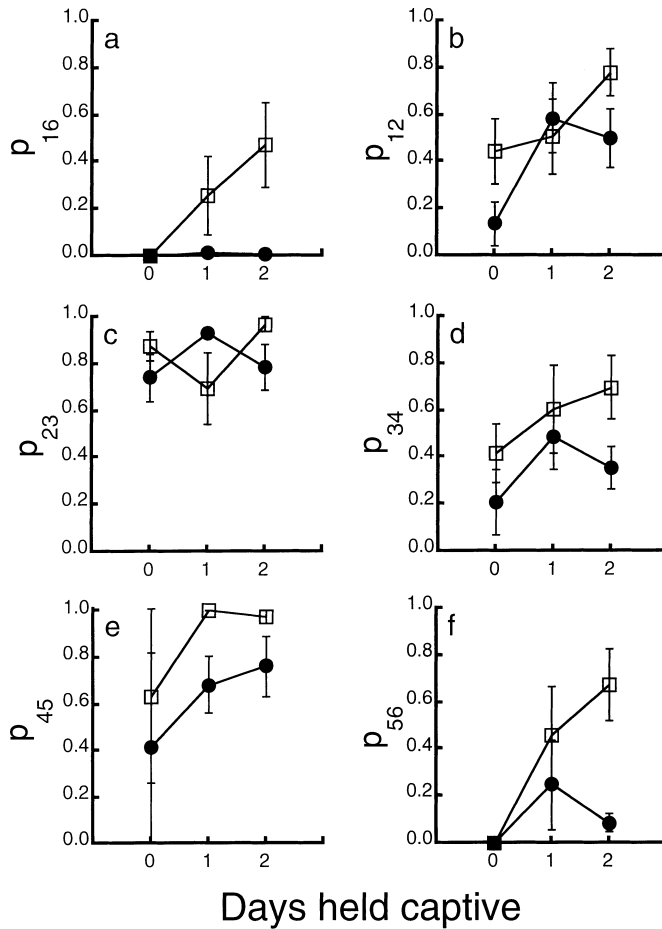
*Fig. 2:* Six transition probabilities with $\pm$ SE. (a) $p_{16}$, sample sizes: swim, 0 d (n = 6); control, 0 d (n = 6); swim, 1 d (n = 6); control, 1 d (n = 6); swim, 2 d (n = 6); control, 2 d (n = 6). (b) $p_{12}$, sample sizes: 6, 6, 6, 6, 6, 6. (c) $p_{23}$, sample sizes: 5, 4, 6, 5, 6, 5. (d) $p_{34}$, sample sizes: 5, 4, 5, 5, 6, 5. (e) $p_{45}$, sample sizes: 4, 2, 4, 5, 6, 5. (f) $p_{56}$, sample sizes: 4, 1, 4, 5, 6, 5. Open squares, swim females; closed circles, control females

initiation to entering a nest. This matches the conclusion of Milinski & Bakker (1992) that female threespine stickleback choosiness declined when female energy or time were limited. Our protocol allowed us to examine where in the mate-choice process the swimming and holding-time manipulations affected female behavior.

We found that the swimming manipulation significantly affected the last two transitions in the mate-choice process ($p_{45}$ and $p_{56}$) and that the holding-time manipulation significantly affected the first and last transition ($p_{12}$ and $p_{56}$). These results suggest that the mate-choice process for female threespine stickleacks is state-dependent in complex, non-uniform, ways. In other words, the manipula-

tions affected different steps of the process and neither manipulation significantly affected all of the steps. As a consequence, the process would be misunderstood either by looking at it uniformly or by looking at only one portion of the process. It also appears that the two manipulations affected the process differently. In two cases, only one of the two manipulations significantly affected a transition probability. Gravid females that were held for more days were more likely to engage in courtship ($p_{12}$), but the swimming manipulation did not have a significant effect. Conversely, females that swam against a current were more likely to place their snout into a male's nest when at the nest ($p_{45}$), but the holding-time manipulation did not have a significant effect. These tests had weak to moderate power (Table 2), so while there is suggestive evidence that the manipulations affected $p_{12}$ and $p_{45}$ differently, we must conclude so with caution. Nevertheless, our results suggest that looking within the mate-choice process yields insights into how female state alters mate-choice behavior.

Approaches that focus solely on which males are chosen as mates are well-suited for measuring sexual selection for male traits and female preferences for male traits, as aggregated across the steps of mate-finding, mate-assessment, and mate-selection. However, they are limited in what they can tell us about the mechanisms of how one male is chosen over others. Our approach, examining how the transitions between steps in mate-choice are affected by female state, produces a better mechanistic understanding of the mate-choice process. Using this mechanistic understanding of mate-choice we can draw connections between environmental conditions and mate-choice behavior. By knowing where in the mate-choice process female behavior is state-dependent, we can produce specific predictions about how mate-choice behavior will respond to natural and manipulated environmental conditions. For example, based on our swimming manipulation results we can predict that in conditions leading to lower female energy reserves (e.g. environments with reduced food availability), female threespine sticklebacks will be more likely to complete a courtship by spawning, but not more likely to engage in a courtship.

Another advantage of our approach is that it facilitates investigating the evolution of mating strategies and systems by providing information about how mate-choice progresses and how the steps of the process interact. How female behavior in the mate-choice process is altered by changes in costs and female state can significantly impact the relative importance of male traits and the evolution of reproductive strategies. For example, if female threespine sticklebacks use different male traits for mate-assessment and mate-selection decisions, as has been shown for sage grouse (Gibson 1996) and fiddler crabs (Backwell & Passmore 1996), then our two manipulations may have altered how important those male traits were in determining mating success. Our holding-time manipulation made females more likely to assess a male, conceivably reducing sexual selection for male traits on which mate-assessment decisions are based. Alternatively, both of our manipulations appear to have made females more likely to select a mate (i.e. less discriminating about who they select), conceivably reducing sexual selection for male traits on which mate-selection decisions are

based. Therefore, the way in which female state affects assessment and selection decisions may determine the relative importance of various male traits.

Another example of the need for a mechanistic understanding of the mate-choice process is that the independence of female assessment and mate-selection decisions may affect the evolution of male reproductive strategies and mating systems. The time and effort which females and males expend in the mate-choice process is a product of the likelihood that a courtship sequence starts and the likelihood that it ends with mating. Changes in female state that lead females to be more likely to assess males, but have no effect on the likelihood they select a mate, increase the average time and effort expended by males and females in the mate-choice process and improve the discrimination of female mate-choice (Luttbeg 1996). This has the potential to eliminate low-quality males or males with low energy reserves from attempting to attract mates and could foster male mating strategies that circumvent female mate-choice. However, if a change in female state made them more likely to assess and select a mate, then there may be no effect on the amount of time and effort expended in the mate-choice process and no selection for changes in male reproductive strategies. These issues can only be investigated through a mechanistic understanding of the mate-choice process.

A common view of mate-choice is that females make a single decision about males – mate or reject (Gibson & Langen 1996). However, the process of choosing a mate is certainly more complicated than that. We have presented an approach to studying mate-choice that focuses on the sequence of decisions females make when choosing a mate and how those decisions depend on the female's state. The approach is more difficult than standard mate preference trials and may be difficult to apply to species without regular courtship patterns, but we believe that it is necessary to examine the mate-choice process to further our understanding of sexual selection and the evolution of mating systems.

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