

Rational mate choice decisions vary with female age and multidimensional male signals in swordtails

Luke Reding  | Molly E. Cummings

Department of Integrative
Biology, University of Texas at Austin,
Austin, Texas

Correspondence

Luke Reding, Department of Integrative
Biology, University of Texas at Austin, 1
University Station C0990, Austin, TX 78712.
Email: lukereding@utexas.edu

Funding information

Ecology, Evolution, and Behavior Graduate
Program at University of Texas at Austin;
Animal Behavior Society; National Science
Foundation, Grant/Award Number: DGE-
1110007

Editor: S. Foster

Abstract

Biologists have long been interested in intransitive preferences: circular preferences in which options cannot be ranked and no single option dominates, similar to a game of rock-paper-scissors. Intransitive preferences violate rational decision-making, an assumption made by models of evolution by mate choice. Despite its potential importance in the study of sexual selection, few studies have tested for intransitive preferences. Even fewer have asked whether females differ in whether they choose mates transitively or intransitively and what factors might predict (in)transitive choice. Though intransitive choice is thought to be more common as options become more complex, this prediction is untested in animals. To fill this gap, we tested whether female *Xiphophorus nigrensis* swordtails can rank digitally animated males differing in size, courtship intensity, or both size and courtship intensity, and whether female responses were predicted by a female's age. Females choosing among males that varied only in size showed higher than expected levels of intransitivity, whereas females choosing among males that varied in their courtship or both properties did not. Older females were more likely to be irrational than younger females when evaluating male size, suggesting that experience modifies transitive decision-making processes. These results show that mate choice irrationality may vary by a female's experience and the signal characteristics during decision-making.

KEYWORDS

age-dependence, complex signaling, decision-making, intransitivity, optimality, utility

1 | INTRODUCTION

In 1954, Kenneth May performed a simple but powerful experiment with a classroom of college students (May, 1954). He presented his students with three hypothetical marriage partners that varied in wealth, attractiveness, and intelligence. He created all three possible pairs of these hypothetical partners, which he called x, y, and z: x with y, y with z, and x with z. He then independently presented each student with each pair of hypothetical partners and asked which of the two potential partners in each pair the student preferred. When May tallied up the students' responses, he found that some of the students showed intransitive, rock-paper-scissors-like preferences: for these students, there was no most attractive

partner. Rather, the attractiveness of a given partner depended on the other partner she was paired with (her "choice set" or "choice environment").

Intransitive preferences like those that May described in humans are of interest to both biologists and economists because they imply irrationality: the idea that options cannot be ranked consistently on a univariate scale (Kacelnik, 2006; Kirkpatrick, Rand, & Ryan, 2006; Luce, 1959). Irrationality implies that choosers are not independently evaluating the available options but are instead comparing among options. Although there are other consequences of rationality, perhaps the most fundamental hallmark of rational behavior is transitivity—the ability of a chooser to form an internally consistent ranking of her options (Bateson & Healy, 2005; Luce,

1959). Intransitivities—circular, rock-paper-scissors-like preferences in which no option is best—imply irrational behavior. Because we only focus on intransitivities, and not all aspects of irrationality, we use “irrational” and “intransitive” interchangeably throughout this paper.

Critically, classic models of economic decision-making (i.e., expected utility theory) assume that humans make rational, and thus transitive, decisions (Luce, 1959; May, 1954; von Neumann & Morgenstern, 1944); violations of rationality imply that the assumptions underlying economic models might not accurately reflect how humans actually make choices. Findings by May and others on irrational choice behavior catalyzed a number of studies in humans documenting the presence of irrationality (Kahneman, 1994), leading to the development of models that relaxed rational assumptions of utility theory and creating the field of behavioral economics (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992).

Although perhaps unrealized for some time, models of animal behavior and evolutionary models of sexual selection make the same rationality assumptions as economic models (Bateson & Healy, 2005; Kirkpatrick et al., 2006). Models of optimal foraging and mate choice assume that animals are maximizing some function by making the choices they do. For example, models of sexual selection by female choice assume that a female's preference can be adequately described by a preference function that—independently of other males under consideration—maps a given male to some preference value (Bateson & Healy, 2005; Kirkpatrick et al., 2006). Females choose the male that maximizes this preference function. A female may fail to exhibit such a preference function if, for example, her preferences are context-dependent and her preference for a given male depends on the other potential mates she has sampled.

While assuming females act as though maximizing some preference function may seem reasonable, the studies alluded to above in humans suggest that organisms can often choose irrationally. Findings of irrationality in animal mate choice would suggest that core assumptions underpinning our understanding of sexual selection by female choice may be flawed, and thus the realism of the models limited (Ryan, Akre, & Kirkpatrick, 2007). Intransitive mate choice would also provide a largely unexplored mechanism that could maintain male polymorphism within populations and possibility accelerate divergence between populations (Kirkpatrick et al., 2006).

Studies of rationality in animals have usually only focused on foraging and mate choice. These studies suggest that animals often do not choose food and mates in a rational way (Bateson, 2002; Bateson, Healy, & Hurly, 2002; Latty & Beekman, 2011; Lea & Ryan, 2015; Locatello, Poli, & Rasotto, 2015; Navarick & Fantino, 1972; Reaney, 2009; Shafir, 1994). We focus here on mate choice irrationality. While many of these studies provide evidence that choices are context-dependent, few studies directly test for mate choice transitivity. Kirkpatrick et al. (2006) found that túngara frogs were not strictly transitive in their preferences, but also did not show clear evidence for intransitivity. Meanwhile, other studies have found support for transitive female mate choice. Dechaume-Moncharmont,

Freychet, Motreuil, and Cézilly (2013) found that convict cichlid females were transitive in their preferences for males that varied in their size. Arbuthnott, Fedina, Pletcher, and Promislow (2017) found that male mate choice for 10 isogenic lines of *Drosophila melanogaster* was nearly perfectly transitive.

The majority of rationality studies to date treat the population, not the individual, as the level of interest (for exceptions see Dechaume-Moncharmont et al., 2013; Shafir, 1994). For example, the *Drosophila* study tested each male in a single binary test, not multiple tests, generating group-level preferences for each of the female lines instead of individual-level preferences (Arbuthnott et al., 2017). Gabel and Hennig (2016) tested female crickets multiple times for their mating preferences, but calculated population-level preferences. Why does the level of analysis matter? First, individuals, not populations, choose mates. Studying mate choice at the individual level is more natural and gives us greater insight into how female behavior influences evolutionary outcomes. Second, just as females can vary in their mating preferences, females may vary in their transitive decision-making. One can imagine that a population in which some females choose mates transitively, others intransitively, may have different characteristics and evolutionary trajectories than a population in which all females choose transitively or intransitively. Studying transitivity at the group level masks this variation. Third, by studying transitivity behavior at the level of the individual, we can begin to identify inherent characteristics of the chooser (e.g., experience) that predict individual decision-making behaviors.

It might be normal to assume that a population of transitive choosers will also be transitive at the level of the population, but a simple exercise shows that this reasoning is flawed. Imagine for simplicity there are three individuals in a population. Each is transitive. The first shows the ranking $A > B > C$ for some arbitrary options A, B, and C, where the option to the left of the “>” is preferred. The second shows $B > C > A$ and the third $C > A > B$. Though each chooser is transitive, at the group level, the preferences appear intransitive: $A > B > C > A$. This phenomenon, known as Condorcet's paradox or the voting paradox (marquis de Condorcet, 1785), shows that there is no clear correspondence between individual- and group-level transitivity (Regenwetter, Dana, & Davis-Stober, 2011). Studying transitivity at the level of the group may therefore give us a skewed perspective of how females are actually choosing mates.

Most studies of intransitivities in animals stop at documenting the presence of irrational behavior. Many basic questions about transitive choice in animals thus remain unasked, despite being crucial for understanding the evolutionary consequences of irrational mate selection. As noted above, the focus on population-level preferences means that our understanding of the variation of transitive choice in populations is extremely limited, though this variation is critical to understanding the potential evolutionary consequences of irrational mate choice. If we can begin to predict under what conditions females are intransitive, or what inherent properties of the chooser predict transitive tendencies, we might be in a better position to create more realistic models of how females choose mates and predict more accurate trajectories of evolution by sexual selection.

To date, studies have been largely silent on what the potential causes of intransitive behavior might be. Is intransitive behavior an inherent property of the chooser? Can it be modified by experience? Or is it simply a property of the different options presented and how these options differ? The latter possibility suggests that irrationality depends more on the specifics of the choice and less on the innate properties specific to a given chooser. For example, it has been suggested that when mates differ in many ways, it becomes more difficult to combine all the features of potential mates into a single "score" needed to fulfill the tenants of rational decision-making (Bateson & Healy, 2005). Thus, we would predict greater irrational behavior when mates differ in many ways (e.g., size, behavior, etc.). While this idea has been tested in a foraging context with hummingbirds, which still show some evidence of irrational choice when food options only differ in a single way (Morgan, Hurly, Bateson, Asher, & Healy, 2012), this prediction remains untested in the context of mate choice.

Whether an individual chooses in a transitive or intransitive way could also be an inherent property of the chooser. For example, an individual's experiences may shape an individual's propensity to choose rationally or irrationally. While experience often plays a role in decision-making (Bakker & Milinski, 1991; Collins, 1995; Hebets, 2003; Wagner, Smeds, & Wiegmann, 2001), the role of experience in rationality is unstudied. Examinations of experience-based rationality in humans have provided conflicting results. Children become more rational over time in their preferences for colors (Bradbury & Moscato, 1974, 1982). However, a recent study found that older individuals are more susceptible to the decoy effect, a phenomenon related to intransitivity, in a task involving choosing rectangles of different sizes (Zhen & Yu, 2016). This suggests that greater experience may increase irrational decision-making for specific traits. These conflicting results suggest a complex relationship between experience or age and decision-making processes. Additionally, how an individual explores a choice environment may have some bearing on whether she makes transitive or intransitive choices.

In order to understand under what conditions irrational behavior occurs, what causes irrational behavior, and whether we can predict its presence, we need a deeper understanding of how variation among individuals maps to their choice behavior. Here, we study rationality of mate choice in swordtail (*Xiphophorus nigrensis*) females. We test how different male traits affect the variation in rationality among females and whether transitivity can be modified with experience. Swordtails have been a model system for the study of female choice for decades (Ryan & Causey, 1989; Ryan, Hews, & Wagner, 1990; Zimmerer & Kallman, 1989). Across swordtail species, males show diverse phenotypes (coloration; presence of vertical bars; presence of an extension of the caudal fin called the sword; courtship behavior) that likely evolved in response to selection by females. In *X. nigrensis* swordtails, males have a genetic polymorphism that produces alternative male phenotypes with different sizes and behavioral traits: large males court females, small males attempt coercive matings with females, and intermediate males show both behaviors (Ryan & Causey, 1989). In general, females strongly and consistently prefer large, courting males over small, coercive males (Cummings & Mollaghan, 2006; Wong, So,

& Cummings, 2011), yet this preference has recently been shown to be context-dependent (Reding & Cummings, 2017).

There are many advantages of using swordtails to test for individual-level mate choice transitivity. First, association preference, a relatively simple measure of female time spent near different male options, has been well documented to predict male mating success (in the related species *X. helleri*; Walling, Royle, Lindström, & Metcalfe, 2010), correlates with female receptivity displays (in *X. nigrensis*; Cummings & Mollaghan, 2006), and is stable over a female's reproductive cycle (in *X. nigrensis*; Ramsey, Wong, & Cummings, 2011). This contrasts with other poeciliid fish where cryptic female choice can obscure the use of proximity measures as a proxy for preference (*Poecilia reticulata*; Pilastro, Simonato, Bisazza, & Evans, 2004). Additionally, *X. nigrensis* have been shown to discriminate between male options (large courting vs. small coercive types) with male animations in the same way they do with live stimuli, but with much higher repeatability ($r = 0.32$ with live stimuli, Cummings & Mollaghan, 2006; $r = 0.74$ with male animations; Reding & Cummings, 2017). This natural and repeatable response to animated stimuli is a powerful tool for transitivity studies where researchers need to both test subjects across multiple trials and ensure that all subjects experience each stimulus in the same way. For instance, in a study designed to test for transitivity of size preferences with live stimuli, one female may view a large male that actively courts her, while in a different trial a female observes a large male that barely notices her. The use of synthetic stimuli allows researchers to isolate which male features females prefer as well as identify patterns of transitivity with greater confidence.

We present swordtail females with digitally animated males that vary in their size, courtship intensity, or both size and courtship intensity (as in Reding & Cummings, 2017). We score female preferences for each type of male in dichotomous choice trials, similar to May's round-robin experiment in humans. First, we document individual variation in rational decision-making behavior among swordtails. Second, we test whether the complexity of the choice environment predicts the prevalence of irrationality. For this we test whether females are more likely to make irrational decisions when males vary in multiple attributes relative to when males vary in a single way (e.g., size). Finally, we examine whether rational decision-making behavior is a function of a female's age (experience) or her exploratory tendencies. For this we test whether female size, a surrogate for age in this species (Morris & Ryan, 1990), as well as her sampling strategy during the experimental trials is related to transitive decision-making.

2 | METHODS

2.1 | Fish husbandry

All fish were descendants of wild-caught *X. nigrensis* (from the Nacimiento de Río Choy in San Luis Potosí, Mexico) and housed in semi-natural conditions at Brackenridge Field Laboratories at the University of Texas at Austin. All females were isolated from males

for at least 2 weeks prior to testing to ensure sexual motivation but were housed with another female for social companionship. Females were fed prior to testing. Experimental procedures were approved by the Institutional Animal Care and Use Committee at the University of Texas at Austin (protocol number AUP-2013-00156).

2.2 | Choice assays

The individual-based analysis presented here is drawn from a previously published dataset that examined context-dependent choices at the population level (Reding & Cummings, 2017) and we refer interested readers to the expansive methods section of that publication. In brief, we tested female *Xiphophorus nigrensis* swordtails for transitive preferences when choosing dichotomously between male animations that differ in only size, only courtship, or both size and courtship. Nineteen females were tested in the size-only experiment, 17 in the courtship only, and 29 in the experiment where male animations differed by size and courtship (this included five females from the size-only trials, 10 females from the courtship-only trials, and 14 females that were naïve to preference trials; see Reding & Cummings, 2017). Three animations were created for each choice experiment that represented a range of a single trait (small, medium, or large sizes for the size-only experiment; no, low-, or high-courtship for the courtship only experiment) or a specific combination of traits (small size with high courtship, intermediate size with intermediate courtship, large size with no courtship). For each of the choice experiments, females experienced three choice trials with all possible pairings of the three male stimuli in randomized order and 5–14 days between tests. By comparing a female's choices between experiments, we were able to determine if female *X. nigrensis* are more likely to form a transitive ranking of males when given a simple choice in which males differed in just one dimension—their size or courtship intensity—compared to a more complex choice in which both the size and courtship intensity of males were varied.

Similar to other studies of rationality with digitized acoustic stimuli (Gabel & Hennig, 2016; Lea & Ryan, 2015), we used digital animations of males in our tests for transitivity. Why is this important? May, in the study described in the Introduction (May, 1954), used imaginary, artificial partners for a reason: each partner was presented the same way to each chooser. Using somewhat artificial options allows for cleaner, more straightforward comparisons across the choosers. In particular, a male's behavior toward a female affects her strength of preference for that male in this species (Wong et al., 2011). Creating animations of males allowed us to keep a male's behavior invariant while changing a different aspect of his phenotype. By artificially synthesizing males, each of the males appeared the same to each female, allowing us to more confidently compare preferences across females.

We synthesized animations of male *X. nigrensis*, created from a video of a single large male exemplar courting a female, to precisely control for male appearance and behavior. We conducted two experiments where we presented females with a pair of male

animations that varied along a single dimension (either size-only or courtship-only; Figure 1a) and a third experiment where we presented females with a pair of males that differed in both dimensions (size and courtship; Figure 1a). In the size comparison experiment, we synthesized three animated males that shared the same body shape, coloration, and low-level courtship vigor, but varied in their body size. While controlling for behavior and appearance, the sizes of the animated males corresponded to typical sizes of the alternative male classes of this species (small males were 21.5 mm in standard length, intermediate males 28.75 mm, and large males 36 mm) (Ryan & Causey, 1989). In the courtship experiment, we created animations using the same body size (28.75 mm), shape, and color, but varied the male's courtship intensity (none, low- or high-level vigor). In the third, multivariate experiment, females were presented with animations in which both male size and courtship intensity varied (Figure 1a). Population-level preferences for every pair of males in each experiment are given in a previous publication (Reding & Cummings, 2017).

In each experiment, every female was tested three times, each with a different combination of males (Figure 1a), similar to a round-robin tournament. This design allows us to test whether females form a consistent, transitive ranking of males or whether preferences are intransitive. We measured female mating preferences as the proportion of time a female spent near each male, which likely indicates her mating intent (Walling et al., 2010). Female time spent near each male has been shown to be a repeatable measure using live stimuli in this species (Cummings & Mollaghan, 2006); the repeatability estimate more than doubles when using digitally animated male stimuli with controlled appearance and behavior (Reding & Cummings, 2017). We assumed that if a female spends more time with a male, that male is preferred (e.g., time associating with preferred male is >50% of total association time, while time associating with less preferred male is <50% total association time). This is a common assumption in studies of transitivity (Appleby, 1983; Kirkpatrick et al., 2006). Using a stricter cut-off for preference would have resulted in a greatly diminished sample size, especially because each female was tested three times and thus failure to meet the criteria on a single test would be the result in that female's exclusion from the study. Additionally, a previous publication using this same experiment (Reding & Cummings, 2017) showed clear population-level preferences in some of the choices presented to females. Based on a female's pattern of preferences in the three choice tests, we classified each female as transitive or intransitive in her mating preferences. For each experiment, there were six possible transitive rankings and two possible intransitive rankings (see Figure 1b for examples). We used a variation of a validated tracking script (Reding & Cummings, 2016) to extract the coordinates of the fish in the tank throughout the trial. We defined three zones: two in front of each screen showing the male animations and one around the artificial plant that provided refuge for the fish.

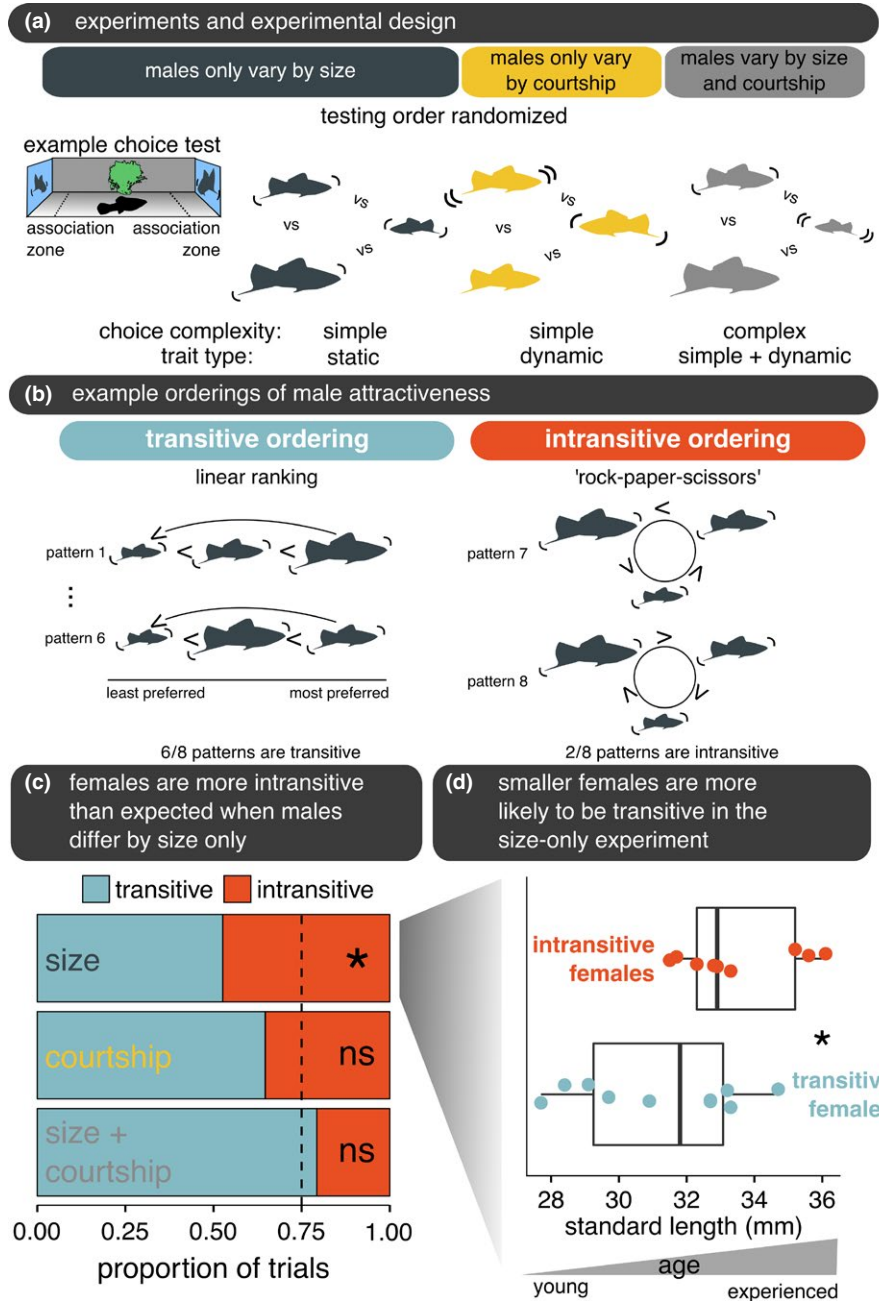


FIGURE 1 (a) Experiments and experimental design. An example choice test is shown on the left with dotted lines marking boundaries of the association zones. Blue represents the experiment where males only varied by size, yellow where males varied only by courtship behavior, and grey where males varied both by size and courtship behavior. Females were tested three times, each with a different set of males. Males shown vary in their size and courtship intensity. The number of “)” enclosing each male indicates his courtship level: none for no courtship, “)” for low-level courtship, and “))” for high-level courtship. Test order was randomized for each female. (b) Examples of a transitive ordering (left, light blue) and intransitive ordering (right, red). The wide end of the > points to the preferred male. There are a total of six possible transitive orderings; only two are shown here due to space limitations. (c) Proportion of transitive and intransitive females in each of the three experiments. If females choose at random, then 75% of the time they will choose transitively because six of the possible eight patterns of preference a female could exhibit in the experiment are transitive. (d) Smaller females are more likely to be transitive in the size-only experiment. Smaller females are younger in this species since growth in females is indeterminate. * $p < 0.05$, while “ns” indicates a non-statistically significant result. [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Statistics

All statistics were carried out in R version 3.4.1 (R Core Team, 2017). We used binomial tests to test whether the number of intransitive females differed from the null expectation of 25% if females choose randomly. We used non-parametric, two-sample permutations tests using the coin package (Hothorn, Hornik, van de Wiel, & Zeileis, 2006) to test whether female sizes were equivalent between transitive and intransitive females in each of the three experiments. We used a mixed-effects model to test whether larger individuals were more exploratory. Experiment type and standard length were fixed effects, individual female was a random effect (because some females were tested in two experiments), and total distance traveled in pixels was the response variable. All tests were two-tailed, and

packages in the tidyverse (Wickham, 2017) collection of R packages were used to reshape, transform, and visualize the data.

3 | RESULTS

We first tested whether female swordtails could rank digitally manipulated males, as required by rational choice, when males differed in their size, courtship vigor, and both size and courtship. When shown male animations in which males varied only by size, more females were intransitive than expected by chance: 53% of females were transitive compared to a null expectation of 75% (9 intransitive, 10 transitive; binomial test; $p = 0.033$; Figure 1c; two of the eight possible patterns of preference are intransitive). In contrast, females

exposed to males that only differed in courtship vigor did not show a level of intransitivity that differed from a null expectation (65% transitive females; six intransitive, 11 transitive; $p = 0.400$). Finally, contrary to our prediction, we found that when males varied in both size and courtship, females were no more intransitive than would be expected by chance (79% transitive females; six intransitive, 23 transitive; $p = 0.674$).

To test whether transitivity status may be altered by experience, we next tested whether female standard length, a surrogate for age in this species, was related to transitivity status. When females chose among males that differed only in size, we found that intransitive females were on average larger and therefore older than transitive females (average difference in standard lengths (intransitive - transitive fish): 2.25 mm; permutation test; $Z = 2.081$; $p = 0.0343$; Figure 1d), suggesting that females become more intransitive in choosing males based on size as they age. The other two experiments showed no such age-based differences (courtship experiment: average difference: 0.40 mm; $Z = 0.343$, $p = 0.747$; size and courtship experiment: average difference: -1.08 mm; $Z = -0.901$, $p = 0.380$). In other fish species, size and exploration are related (e.g., Brown & Braithwaite, 2005). Thus, the differences in decision-making in the size-only experiment may be driven by underlying differences in the exploration rate. There was no statistically significant relationship, however, between the standard length of a female and the total distance she traveled in the tank during the trial (effect of standard length: $X^2_1 = 0.721$, $p = 0.396$).

4 | DISCUSSION

We used animations of male swordtails to show that females are largely transitive in their choice of mates but are more intransitive than expected by chance when potential males varied only in their size. In this same experiment, young females tended to choose more transitively than older females, suggesting that decision rules may change with age or experience.

Females showed greater intransitivity than expected by chance when faced with a relatively simple choice between males that varied in their size, but not when males varied in courtship intensity. Why might this be? Size is a static trait in swordtail males—unlike females, males stop growing once they are sexually mature (Kallman, 1989)—while courtship is a dynamic trait. Interestingly, static traits like male size have been predicted to be less informative to females than more dynamic traits since static traits do not respond quickly to changes in male health or condition (Kodric-Brown & Nicoletto, 2001; Ligon & Zwartjes, 1995). Male courtship vigor has been linked to condition in a number of taxa (Gibson & Uetz, 2008; Hoefler, Persons, & Rypstra, 2008; Kim & Choe, 2003; Kotiaho, 2000). In this study, when courtship—a dynamic trait—varied among the potential males, females were no longer more intransitive than expected. This raises the intriguing possibility that the evolution of courtship facilitated more rational, consistent decisions among females for her choice of mate. It also suggests that

the type of traits displayed by males—static and/or dynamic—may shape the decision processes of females, and thus the effect that intransitive choice has on the evolution of the population. Perhaps irrational mate choice is more likely in species in which the traits males use to attract females tend to be static and not dynamic.

The prevailing literature on rationality in animals suggests that rational decision-making should be more difficult when the options vary in more ways (Bateson & Healy, 2005). Curiously, we find an overabundance of irrationality when females choose between males that only differ in their size. Why might this be? Size and courtship predictably co-vary in swordtail males: large males court females while small males sneak copulations (Ryan & Causey, 1989). Identifying the attractive large male should be an easy task when a female is presented with live males where male size and behavior are correlated. When males only differ in one way, however, it may be more difficult to discriminate between males, and this may lead to greater number of intransitive fish in this experiment.

We found that older females were more likely to be intransitive, and therefore irrational, than younger females when males varied only in size. This result suggests that experience may modify choice rules by making them more irrational. *X. nigrensis* females likely learn about the different male size morphs as they age (Wong et al., 2011); our results are consistent with the idea that learning may play some role in the development of intransitive choice behavior. These results parallel some studies in the human literature showing that humans are more likely to be susceptible to the decoy effect—an effect related to intransitivity—if they are older than if they are younger. Similar to our study, when humans were given options that differed in size, older individuals were more irrational than younger individuals (Zhen & Yu, 2016). It's possible that in both humans and fish, experience and learning tweak rational decision rules for options that differ in static traits, like size.

Our finding of potential age-dependent intransitive mate choice also has implications for understanding the evolutionary effects of intransitive choice in populations. It is possible, for example, that the age structure of females affects the strength of overall mate choice intransitivity within populations. In populations with older females, intransitive mate choice may be more prevalent and thus have a larger effect on evolutionary processes, for example by increasing the diversity of male morphs. The effects of intransitive choice may be more muted in younger populations. Overall, our findings suggest that incorporating age structure into studies of mate choice intransitivity and sexual selection more generally may provide a more holistic understanding of how sexual selection affects evolution. While some empirical (Coltman, Festa-Bianchet, Jorgenson, & Strobeck, 2002; Wong et al., 2011) and theoretical (Adamson, 2013; Kokko, 1997; Proulx, Day, & Rowe, 2002) studies have begun to explore the role of age-dependent signaling and age structure in studies of sexual selection, the role of age structure remains a limitation of current models of sexual selection.

Mating preferences are usually studied at the population level. We explicitly explore variation in rational decision-making at the individual level for a number of reasons. First, as mate choice decisions

are made at an individual basis and not through group consensus, studying mate choice at the individual level is more natural and makes fewer assumptions (e.g., that all females have similar preferences). Second, spurious intransitivities can arise from aggregating individual-level responses into group-level patterns. For example, females may be transitive in their preferences, but might vary in which male they consider the best, giving rise to group-level intransitive preferences. Studying patterns of preference at the individual-level ensures that any observed intransitivities are due to actual intransitive preferences and are not artifacts of aggregation.

We previously analyzed the population-level preferences of the females reported here for the same types of animated males (Reding & Cummings, 2017). What do we gain by taking the individual-level approach advocated here? Viewing our population-level results through the lens of rational choice reinforces our contention that group- and individual-level preferences can tell different stories. At the population level, for a given choice between two males, the population-level preferences often did not differ from zero. At the population-level, this might be viewed as indifference; another way to view this result is that some females preferred one male, others the opposite male. At the population level, there was some evidence that females preferred males of larger size, though our individual-level analyses here reveal that this simple explanation masked some interesting dynamics at the individual level. When we examined this same question of size preference across individual females, we found high levels of intransitivities that were largely explained by a female's age. Ultimately, trying to understand how individual females behave from population-level data is like trying to describe a face based only on the shadow it casts; the subtleties and details are masked by the abstraction.

What are the evolutionary implications of individual variation in rational mate choice decision-making processes? One possibility is that variation in female mate choice rules may contribute to the maintenance of male polymorphism within populations. Just as ecological competitive intransitivities in communities increase species diversity (Laird & Schamp, 2006; Soliveres et al., 2015), it is clear that similar processes in female mate choice intransitivities should increase male phenotypic diversity. Unfortunately, there are no studies to our knowledge that attempt to quantify how the presence of intransitive females influences male phenotypic diversity. While a balance between natural and sexual selection is expected to maintain the three-male polymorphism in this species (Ryan, Pease, & Morris, 1992), our results suggest that irrational female mating preferences for size alone may play some role in maintaining these different male morphs. Thus, intransitive mate choice may provide a partial solution to the lek paradox, the finding that in many taxa males have high additive genetic variance for mating traits even in the face of female choice (Pomiankowski & Moller, 1995).

More generally, however, the evolutionary consequences of mate choice intransitives are unexplored. We show that a key assumption of models of sexual selection, rational choice by females, may be violated in swordtail females. This violation was most pronounced among older females when males differed only in size. With

this study, we begin to move beyond documenting that irrationality exists for decisions essential to an animal's fecundity by identifying the factors that predict irrationality at the individual level. This study underscores that females can vary in rational decision-making tendencies and that models of sexual selection should be relaxed to incorporate findings of context-dependent behavior in mate choice to better characterize how female choice behavior may influence the direction of secondary sexual trait evolution and the maintenance of male polymorphisms.

ACKNOWLEDGEMENTS

We thank the members of the Cummings lab for critiques of an early draft and Brackenridge Field Laboratory for housing the fish used in this experiment. We thank the Mexican National Commission of Aquaculture and Fisheries (2009; permit DGOPA.07311.130709.-2261) for collection permits. This research was funded by a student research award through the Animal Behavior Society, the DDIG-like award from the Ecology, Evolution, and Behavior program at the University of Texas at Austin, and a National Science Foundation Graduate Research Fellowship (DGE-1110007) to L.R.

ORCID

Luke Reding  <http://orcid.org/0000-0002-1808-9125>

REFERENCES

- Adamson, J. J. (2013). Evolution of male life histories and age-dependent sexual signals under female choice. *PeerJ*, 1, e225. <https://doi.org/10.7717/peerj.225>
- Appleby, M. C. (1983). The probability of linearity in hierarchies. *Animal Behaviour*, 31(2), 600–608. [https://doi.org/10.1016/S0003-3472\(83\)80084-0](https://doi.org/10.1016/S0003-3472(83)80084-0)
- Arbuthnott, D., Fedina, T. Y., Pletcher, S. D., & Promislow, D. E. L. (2017). Mate choice in fruit flies is rational and adaptive. *Nature Communications*, 8, 13953. <https://doi.org/10.1038/ncomms13953>
- Bakker, T. C. M., & Milinski, M. (1991). Sequential female choice and the previous male effect in sticklebacks. *Behavioral Ecology and Sociobiology*, 29(3), 205–210. <https://doi.org/10.1007/BF00166402>
- Bateson, M. (2002). Context-dependent foraging choices in risk-sensitive starlings. *Animal Behaviour*, 64(2), 251–260. <https://doi.org/10.1006/anbe.2002.3059>
- Bateson, M., & Healy, S. D. (2005). Comparative evaluation and its implications for mate choice. *Trends in Ecology & Evolution*, 20(12), 659–664. <https://doi.org/10.1016/j.tree.2005.08.013>
- Bateson, M., Healy, S. D., & Hurly, T. A. (2002). Irrational choices in hummingbird foraging behaviour. *Animal Behaviour*, 63(3), 587–596. <https://doi.org/10.1006/anbe.2001.1925>
- Bradbury, H., & Moscato, T. (1974). Transitivity and the patterns of children's preferences. *Developmental Psychology*, 10(1), 55–64. <https://doi.org/10.1037/h0035538>
- Bradbury, H., & Moscato, M. (1982). Development of transitivity of preference: Novelty and linear regularity. *The Journal of Genetic Psychology*, 140(2), 265–281. <https://doi.org/10.1080/00221325.1982.10534199>

- Brown, C., & Braithwaite, V. A. (2005). Effects of predation pressure on the cognitive ability of the poeciliid *Brachyraphis episcopi*. *Behavioral Ecology*, 16(2), 482–487. <https://doi.org/10.1093/beheco/ari016>
- Collins, S. A. (1995). The effect of recent experience on female choice in zebra finches. *Animal Behaviour*, 49(2), 479–486. <https://doi.org/10.1006/anbe.1995.0062>
- Coltman, D. W., Festa-Bianchet, M., Jorgenson, J. T., & Strobeck, C. (2002). Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London B: Biological Sciences*, 269(1487), 165–172. <https://doi.org/10.1098/rspb.2001.1851>
- Cummings, M., & Mollaghan, D. (2006). Repeatability and consistency of female preference behaviours in a northern swordtail, *Xiphophorus nigrensis*. *Animal Behaviour*, 72(1), 217–224. <https://doi.org/10.1016/j.anbehav.2006.01.009>
- Dechaume-Moncharmont, F.-X., Freychet, M., Motreuil, S., & Cézilly, F. (2013). Female mate choice in convict cichlids is transitive and consistent with a self-referent directional preference. *Frontiers in Zoology*, 10, 69. <https://doi.org/10.1186/1742-9994-10-69>
- Gabel, E., & Hennig, R. M. (2016). Evidence for comparative decision making in female crickets. *Behavioral Ecology*, 27, 1216–1222. <https://doi.org/10.1093/beheco/arw030>
- Gibson, J. S., & Uetz, G. W. (2008). Seismic communication and mate choice in wolf spiders: Components of male seismic signals and mating success. *Animal Behaviour*, 75(4), 1253–1262. <https://doi.org/10.1016/j.anbehav.2007.09.026>
- Hebets, E. A. (2003). Subadult experience influences adult mate choice in an arthropod: Exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences of the United States of America*, 100(23), 13390–13395. <https://doi.org/10.1073/pnas.2333262100>
- Hoefler, C. D., Persons, M. H., & Rypstra, A. L. (2008). Evolutionarily costly courtship displays in a wolf spider: A test of viability indicator theory. *Behavioral Ecology*, 19(5), 974–979. <https://doi.org/10.1093/beheco/arn055>
- Hothorn, T., Hornik, K., van de Wiel, M. A., & Zeileis, A. (2006). A lego system for conditional inference. *The American Statistician*, 60(3), 257–263. <https://doi.org/10.1198/000313006X118430>
- Kacelnik, A. (2006). Meanings of rationality. In S. Hurley, & M. Nudds (Eds.), *Rational Animals* (pp. 87–106). Oxford, UK: Oxford University Press.
- Kahneman, D. (1994). New challenges to the rationality assumption. *Journal of Institutional and Theoretical Economics (JITE)/Zeitschrift Für Die Gesamte Staatswissenschaft*, 150(1), 18–36.
- Kahneman, D., & Tversky, A. (1979). Prospect theory: An analysis of decision under risk. *Econometrica: Journal of the Econometric Society*, 47(2), 263–291. <https://doi.org/10.2307/1914185>
- Kallman, K. D. (1989). Genetic control of size at maturity in *Xiphophorus*. In G. K. Meffe, & F. F. Snelson (Eds.), *Ecology and evolution of Livebearing Fishes (Poeciliidae)* (pp. 163–185). Englewood Cliffs, NJ: Prentice-Hall.
- Kim, T. W., & Choe, J. C. (2003). The effect of food availability on the semilunar courtship rhythm in the fiddler crab *Uca lactea* (de Haan) (Brachyura: Ocypodidae). *Behavioral Ecology and Sociobiology*, 54(3), 210–217. <https://doi.org/10.1007/s00265-003-0614-3>
- Kirkpatrick, M., Rand, A. S., & Ryan, M. J. (2006). Mate choice rules in animals. *Animal Behaviour*, 71(5), 1215–1225. <https://doi.org/10.1016/j.anbehav.2005.11.010>
- Kodric-Brown, A., & Nicoletto, P. F. (2001). Female choice in the guppy (*Poecilia reticulata*): The interaction between male color and display. *Behavioral Ecology and Sociobiology*, 50(4), 346–351. <https://doi.org/10.1007/s002650100374>
- Kokko, H. (1997). Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology*, 41(2), 99–107. <https://doi.org/10.1007/s002650050369>
- Kotiaho, J. S. (2000). Testing the assumptions of conditional handicap theory: Costs and condition dependence of a sexually selected trait. *Behavioral Ecology and Sociobiology*, 48(3), 188–194. <https://doi.org/10.1007/s002650000221>
- Laird, R. A., & Schamp, B. S. (2006). Competitive intransitivity promotes species coexistence. *The American Naturalist*, 168(2), 182–193. <https://doi.org/10.1086/506259>
- Latty, T., & Beekman, M. (2011). Irrational decision-making in an amoeboid organism: Transitivity and context-dependent preferences. *Proceedings of the Royal Society of London B: Biological Sciences*, 278(1703), 307–312. <https://doi.org/10.1098/rspb.2010.1045>
- Lea, A. M., & Ryan, M. J. (2015). Irrationality in mate choice revealed by túngara frogs. *Science*, 349(6251), 964–966. <https://doi.org/10.1126/science.aab2012>
- Ligon, J. D., & Zwartjes, P. W. (1995). Ornate plumage of male red junglefowl does not influence mate choice by females. *Animal Behaviour*, 49(1), 117–125. [https://doi.org/10.1016/0003-3472\(95\)80159-6](https://doi.org/10.1016/0003-3472(95)80159-6)
- Locatello, L., Poli, F., & Rasotto, M. B. (2015). Context-dependent evaluation of prospective mates in a fish. *Behavioral Ecology and Sociobiology*, 69(7), 1–8. <https://doi.org/10.1007/s00265-015-1924-y>
- Luce, R. D. (1959). *Individual choice behavior: A theoretical analysis*. Hoboken, NJ: Wiley.
- marquis de Condorcet, M. J. A. (1785). *Essai sur l'application de l'analyse a la probabilité des decisions: rendues a la pluralite de voix*. De l'Imprimerie royale.
- May, K. O. (1954). Intransitivity, utility, and the aggregation of preference patterns. *Econometrica*, 22(1), 1–13. <https://doi.org/10.2307/1909827>
- Morgan, K. V., Hurly, T. A., Bateson, M., Asher, L., & Healy, S. D. (2012). Context-dependent decisions among options varying in a single dimension. *Behavioural Processes*, 89(2), 115–120. <https://doi.org/10.1016/j.beproc.2011.08.017>
- Morris, M. R., & Ryan, M. J. (1990). Age at sexual maturity of male *Xiphophorus nigrensis* in nature. *Copeia*, 1990(3), 747–751. <https://doi.org/10.2307/1446440>
- Navarick, D. J., & Fantino, E. (1972). Transitivity as a property of choice. *Journal of the Experimental Analysis of Behavior*, 18(3), 389–401. <https://doi.org/10.1901/jeab.1972.18-389>
- Pilastro, A., Simonato, M., Bisazza, A., & Evans, J. P. (2004). Cryptic female preference for colorful males in guppies. *Evolution*, 58(3), 665. <https://doi.org/10.1554/03-491>
- Pomiankowski, A., & Moller, A. P. (1995). A resolution of the lek paradox. *Proceedings of the Royal Society of London B: Biological Sciences*, 260(1357), 21–29. <https://doi.org/10.1098/rspb.1995.0054>
- Proulx, S. R., Day, T., & Rowe, L. (2002). Older males signal more reliably. *Proceedings of the Royal Society of London B: Biological Sciences*, 269(1507), 2291–2299. <https://doi.org/10.1098/rspb.2002.2129>
- R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Ramsey, M. E., Wong, R. Y., & Cummings, M. E. (2011). Estradiol, reproductive cycle and preference behavior in a northern swordtail. *General and Comparative Endocrinology*, 170(2), 381–390. <https://doi.org/10.1016/j.ygcen.2010.10.012>
- Reaney, L. T. (2009). Female preference for male phenotypic traits in a fiddler crab: Do females use absolute or comparative evaluation? *Animal Behaviour*, 77(1), 139–143. <https://doi.org/10.1016/j.anbehav.2008.09.019>
- Reding, L., & Cummings, M. E. (2016). Does sensory expansion benefit asexual species? An olfactory discrimination test in Amazon mollies. *Behavioral Ecology*, 27(2), 411–418. <https://doi.org/10.1093/beheco/arv168>
- Reding, L., & Cummings, M. E. (2017). Context-dependent preferences vary by multicomponent signals in a swordtail. *Animal Behaviour*, 129, 237–247. <https://doi.org/10.1016/j.anbehav.2017.05.017>

- Regenwetter, M., Dana, J., & Davis-Stober, C. P. (2011). Transitivity of preferences. *Psychological Review*, 118(1), 42–56. <https://doi.org/10.1037/a0021150>
- Ryan, M. J., Akre, K. L., & Kirkpatrick, M. (2007). Mate choice. *Current Biology*, 17(9), R313–R316. <https://doi.org/10.1016/j.cub.2007.02.002>
- Ryan, M. J., & Causey, B. A. (1989). "Alternative" mating behavior in the swordtails *Xiphophorus nigrensis* and *Xiphophorus pygmaeus* (Pisces: Poeciliidae). *Behavioral Ecology and Sociobiology*, 24(6), 341–348. <https://doi.org/10.1007/BF00293262>
- Ryan, M., Hews, D., & Wagner, W. (1990). Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis*. *Behavioral Ecology and Sociobiology*, 26(4), 231–237. <https://doi.org/10.1007/BF00178316>
- Ryan, M. J., Pease, C. M., & Morris, M. R. (1992). A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: Testing the prediction of equal fitnesses. *The American Naturalist*, 139(1), 21–31. <https://doi.org/10.1086/285311>
- Shafir, S. (1994). Intransitivity of preferences in honey bees: Support for "comparative" evaluation of foraging options. *Animal Behaviour*, 48(1), 55–67. <https://doi.org/10.1006/anbe.1994.1211>
- Soliveres, S., Maestre, F. T., Ulrich, W., Manning, P., Boch, S., Bowker, M. A., ... Allan, E. (2015). Intransitive competition is widespread in plant communities and maintains their species richness. *Ecology Letters*, 18, 790–798. <https://doi.org/10.1111/ele.12456>
- Tversky, A., & Kahneman, D. (1992). Advances in prospect theory: Cumulative representation of uncertainty. *Journal of Risk and Uncertainty*, 5(4), 297–323. <https://doi.org/10.1007/BF00122574>
- von Neumann, J., & Morgenstern, O. (1944). *Theory of games and economic behavior*, Vol. xviii. Princeton, NJ: Princeton University Press.
- Wagner, W. E., Smeds, M. R., & Wiegmann, D. D. (2001). Experience affects female responses to male song in the variable field cricket *Gryllus lineaticeps* (Orthoptera, Gryllidae). *Ethology*, 107(9), 769–776. <https://doi.org/10.1046/j.1439-0310.2001.00700.x>
- Walling, C. A., Royle, N. J., Lindström, J., & Metcalfe, N. B. (2010). Do female association preferences predict the likelihood of reproduction? *Behavioral Ecology and Sociobiology*, 64(4), 541–548. <https://doi.org/10.1007/s00265-009-0869-4>
- Wickham, H. (2017). *tidyverse: Easily install and load "Tidyverse" packages*. Retrieved from <https://CRAN.R-project.org/package=tidyverse>
- Wong, R. Y., So, P., & Cummings, M. E. (2011). How female size and male displays influence mate preference in a swordtail. *Animal Behaviour*, 82(4), 691–697. <https://doi.org/10.1016/j.anbehav.2011.06.024>
- Zhen, S., & Yu, R. (2016). The development of the asymmetrically dominated decoy effect in young children. *Scientific Reports*, 6, <https://doi.org/10.1038/srep22678>
- Zimmerer, E. J., & Kallman, K. D. (1989). Genetic basis for alternative reproductive tactics in the pygmy swordtail, *Xiphophorus nigrensis*. *Evolution*, 43(6), 1298–1307. <https://doi.org/10.2307/2409364>

How to cite this article: Reding L, Cummings ME. Rational mate choice decisions vary with female age and multidimensional male signals in swordtails. *Ethology*. 2018;124:641–649. <https://doi.org/10.1111/eth.12769>