



Original Article

Personality affects female mate choice: frogs displaying more consistent bold behaviors are choosier

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Received 6 June 2023; revised 2 November 2023; editorial decision 7 November 2023; accepted 13 November 2023

Mate choice is an important cause of natural and sexual selection and drives the evolution and elaboration of male ornaments. Yet mate choice decisions are often neither consistent nor uniform, and a range of factors have been identified to influence variation between and within individuals. A potential source of variation influencing preferences and/or choosiness is animal personality, that is, repeatable among-individual differences in behaviors. Not only may individuals differ in average personality phenotype but also vary in how consistently they display said personality. Distinguishing between personality and consistency is important because both aspects are potentially naturally selected traits that may yet influence how sexually selected ornaments are evaluated. Here, we use a predator evasion assay to test whether there is variation in boldness among female gray treefrogs (*Hyla versicolor*), and then examine whether personality traits (spectrum of shy to bold) are correlated with choosiness for longer duration calls. We document substantial and repeatable between-individual variation in boldness, suggesting the presence of animal personality. Results also reveal that the consistency with which females expressed boldness is independent from average personality phenotype and that it is correlated with choosiness: more consistently bold females were choosier.

Key words: boldness, choosiness, mate choice, personality, sexual selection.

INTRODUCTION

The strength and direction of male sexual trait evolution is often dependent upon patterns of female mating decisions (Andersson 1994; Coyne and Orr 2004; Rodríguez et al. 2013). Yet, female mate choice decisions are not necessarily uniform across individuals nor fixed over time, as heritable variation and behavioral flexibility are prevalent both within individuals and among populations (Tobler et al. 2008; Baugh and Ryan 2009). This potential for variation can strengthen selection on male traits or disrupt expected trends by weakening selection through indiscriminate mating choices (Pomiankowski 1987; Chaine and Lyon 2008; Neelon and Höbel 2017). Therefore, exploring potential sources of variation in mate choice decisions could shed light on the adaptive, or maladaptive, aspects of mate choice variation (Bailey and Zuk 2008) and improve the current understanding of the potential evolutionary consequences (Jennions and Petrie 1997).

Between-individual variation in mate choice decisions can arise from two mechanisms: behavioral flexibility or fixed differences in behavior. Many factors can challenge females while making mating

decisions, such as resource availability, social experience, sex ratio, or predator threat, and flexible mate choice may permit the necessary adjustments to maximize fitness (Janetos 1980; Bateson 1983; Partridge and Halliday 1984; Ah-King and Gowaty 2016). Reduced energetic costs and/or survival risks may then balance the increased acceptance rate of less preferred male phenotypes, resulting in more indiscriminate selection patterns (Jennions and Petrie 1997; Cotton et al. 2006; Rosenthal 2017). Alternatively, there may be fixed differences in mate choice, either because the choice criteria themselves are fixed (heritable), or because mate choice decisions are influenced by other stable characteristics or behavioral traits.

One such stable behavioral trait may be animal personality. Broadly, personality refers to repeatable among-individual differences in behaviors such as exploration, boldness, or aggression (Réale et al. 2007; Wolf and Weissing 2010; Dingemanse and Wright 2020). This does not require individuals to be entirely consistent within a behavior; only that the behavior is maintained across replicates (Dingemanse et al. 2010; Wolf and Weissing 2010). Some individuals may maintain different degrees of variability in addition to the traditional personality-like behavior itself; they may differ in their consistency (i.e., in the level of within-individual variation in

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personality). Incorporating within-individual variation as a component distinct from baseline personality traits is not the norm for animal personality studies. However, the concept has been introduced before under a variety of terms, including “intra-individual variability” (Stamps et al. 2012) or “predictability” (Cleasby et al. 2015; O’Dea et al. 2021).

The personality trait of an animal, as well as how consistent it is for that personality trait, affects the way in which it interacts with its environment (Dingemanse and Réale 2005). For example, reactions to predators, food sources, and habitat features, as well as social or sexual interactions with conspecifics and heterospecifics, may vary due to personality (Réale et al. 2007; Peignier et al. 2022). As such, particular personality and consistency types may be favored or disfavored by selection depending on the ecological conditions experienced by the population (Réale et al. 2007). Since individual differences in personality and consistency may result in differences in habitat use, mate-searching strategies, or other aspects involved in mate choice decisions (Martin-Wintle et al. 2017), they may also play a role in sexual selection.

The role of animal personality in mate choice has been investigated extensively from the perspective of whether there are preferences for certain personality types (Godin and Dugatkin 1996; Kwek et al. 2021; Roth et al. 2021; Wang et al. 2022) or whether there is assortative mating based on personality type (i.e., Kralj-Fiser et al. 2013; Pogány et al. 2018; Collins et al. 2019). By contrast, studies examining personality as a potential source of variation on mate choice for sexual traits are rare (but see Sommer-Trembo et al. 2016; Li et al. 2022). Nevertheless, shy and bold females—or more or less consistently shy or bold females—may prefer different ornament values (i.e., differ in peak preference), or they may differ in the willingness to invest effort in obtaining their preferred mate type (i.e., differ in choosiness).

A potential relationship between personality and/or consistency and mate choice decisions may have important evolutionary consequences. Consider that personality is widespread among animals (Finger et al. 2017; Fratkin 2017; Frick et al. 2017; Gartner 2017; Horback 2017; Khan and Echevarria 2017; Waters et al. 2017; Whitham and Washburn 2017) and that it influences survival and reproductive success (Sih et al. 2004; Smith and Blumstein 2008). Thus, selection on personality and/or consistency (e.g., arising from predation regimes) may indirectly cause selection on mate choice, and thereby influence sexual selection on male ornaments. Further, because personality is more continuously expressed (hence, more continuously under selection) than mate choice behaviors, there is a broad range of possible contexts for such influences to arise. Exploring the potential relationships between personality, consistency, and mate choice decisions may bring important evolutionary insights.

Here, we test for relationships between personality, consistency, and female mate choice decisions in Eastern gray treefrogs (*Hyla versicolor*). Anuran amphibians have long been a model system for studying mate choice (i.e., Ryan 1985, 2001; Gerhardt 1991), while exploration of their personality-related traits, particularly in reference to treefrogs (Bisconti et al. 2023) has received comparatively less attention. We used a predator evasion assay replicated four times to test whether females vary in boldness, and then examine whether average boldness, or how consistently females display bold behavior, is correlated with choosiness for longer duration calls. The personality hypothesis makes the prediction that the severity of the escape response varies between females and is repeatable over time. The hypothesis that personality is linked to mate choice

decisions in this species makes the prediction that bolder or more consistent individuals are choosier (i.e., more willing to invest effort in obtaining their preferred mate type).

METHODS

Study species

Eastern gray treefrogs (*H. versicolor*) are a widespread North American frog species (Conant and Collins 1998). Males gather at woodland ponds during the breeding season (May through July) and emit advertisement calls to attract females. In nature, females approach stationary males guided by their calls (termed phonotaxis) and will repeatedly approach speakers broadcasting synthetic stimuli in artificial lab settings (Gerhardt 1992). Female *H. versicolor* display preferences for several call properties, but across their geographical range maintain strongest preference for longer duration calls (Sullivan and Hinshaw 1992; Gerhardt et al. 2000; Reichert and Höbel 2015). Our study population is located near the University of Wisconsin Milwaukee Field Station in Saukville, WI, about 50 min north of the university campus.

During May and June of 2022, we collected females ($n = 58$) from amplexed pairs to ensure sexual receptivity (and hence, willingness to engage in phonotaxis). Female frogs used for mate choice experiments are nearly always collected in amplexus because it ensures that the females are motivated to participate in playback trials (Gerhardt and Doherty 1988; Baugh and Ryan 2009; Bee 2010). Female anuran mate choice behavior is not affected by being engaged in amplexus, nor by the length of time a female was in amplexus before being tested (Murphy and Gerhardt 1996). Then, we transported females to the University of Wisconsin Milwaukee for a series of experiments testing mate choice and personality. While awaiting phonotaxis trials, females were placed in collection boxes (pint-sized Stor-Keeper Freezer Storage Containers) with a centimeter of dechlorinated tap water on the bottom. These were kept in coolers with melting ice to delay oviposition because females become unresponsive to male calls after they lay their eggs. Phonotaxis trials testing choosiness were conducted first (within 3 days after capture) because females remain responsive to mating signals for only a brief period of time. After completing the phonotaxis trials, females were reunited with their mates and placed in 30 cm × 17 cm × 10 cm plastic boxes with one liter of dechlorinated tap water and allowed to oviposit overnight. Thereafter, each female was placed in an individual holding tank to begin the personality experiments and their male counterpart was returned to the collection pond. Experimental procedures were approved by the Animal Care and Use Committee at the University of Wisconsin Milwaukee (Protocol Numbers: 18-19#35 and 21-22#47).

Acoustic playback trials testing choosiness

Stimulus generation

We used the Seewave package (Sueur et al. 2008) in R (Version 3.1.0) to generate two male stimuli differing only by the number of pulses (6 and 18 pulses). Other characteristics of the synthetic advertisement calls mirrored the average call characteristics of the study population: the length of the pulses constituting the call was set as 25 ms, pulse period as 25 ms, call period as 7750 ms, high-frequency peak as 1071 Hz, and low-frequency peak as 2142 Hz (10 dB louder in low frequency) (Reichert and Höbel 2015; Feagles and Höbel 2022a, 2022b).

General playback procedure

All experiments took place inside a semi-anechoic room; the room was dark and maintained at a temperature of 20 ± 2 °C. A circular arena (2-m diameter) created with wire fencing covered in black cloth and foam exercise mats as flooring was set up inside. Artificial call stimuli were presented from JBL Control 1Xtreme speakers, placed facing toward the center of the arena (female's release location) but just outside the arena wall so females could not see them. We adjusted the call amplitude using a 407764 Sound Level Meter (Extech Instruments, RS232/Data logger; C-weighting, fast RMS) also from the center of the arena.

To test for choosiness, we used a two-speaker design (180° angular separation) using a controlled amplitude measured with a Sound Level Meter. One speaker broadcast an unattractive (6 pulse) male call stimulus consistently maintained at 85dB SPL throughout the experiment; the other speaker broadcast an attractive (18 pulse) male call stimulus attenuated in amplitude relative to the unattractive one (Feagles and Höbel 2022a, 2022b). Manipulating amplitude influences the female's perceived distance to the caller, taking advantage of the inverse square law of sound attenuation: a 6 dB decrease in amplitude is equivalent to a doubling of distance from a sound source.

We first tested all frogs at an intermediate amplitude difference (attractive call 12 dB quieter than the unattractive call), but the amplitude difference of subsequent trials depended on each female's previous decision. If she chose the 6 pulse call (less attractive but louder, perceived as closer), we decreased the amplitude difference on her next trial making the task of approaching the more attractive male easier. If the female chose the 18 pulse call (more attractive but softer, perceived as further away), we increased the amplitude difference in her next trial making the task of approaching the more attractive male even more challenging. We repeated this procedure until we had established the highest amplitude difference (measure of choosiness) at which the female still chose the attractive call. Final choosiness score could range between 0 dB and 24 dB (in steps of 3 dB). Each female participated in three or four total trials for one measure of choosiness: a higher amplitude difference indicates a choosier female (choosiest = 24 dB, least choosy = 0 dB).

Predator evasion trials testing personality (boldness)

Experiment husbandry

Each female was placed in an individual holding tank prior to and between the four replicates of the personality experiments (22 × 15 × 14 cm critter cages, equipped with a PVC rod as a perch and one centimeter of dechlorinated tap water on the tank bottom). Before each personality replicate, frogs were given one day for feeding followed by one day of rest. A range of food types was provided over the course of the experiment, but the amount of food was roughly equivalent for each feeding (one medium cricket, one adult mealworm, one large wax worm, or three black soldier fly larvae). Each personality replicate occurred between 1 pm and 5 pm on the third day in the feed–rest–personality sequence. Personality trials were conducted over the span of 12 days (Réale et al. 2007; Niemelä and Dingemans 2018).

Predator evasion assay

The personality experiment measured boldness using severity of escape responses to an approaching novel predator. Methods were modeled after techniques used during physical threat stimulus

tests reviewed by (Kelleher et al. 2018), with modifications to best suit our study species. We confronted each frog with a slowly approaching artificial predator (total height = 26 cm) (see Figure 2A,B). The predator stimulus recreated the shadow effect of a looming predator—a black square with eyespots affixed to the front of a wooden, wheeled children's "Pull Along Duck" toy (BRIO Brand, model 30323, 14cm × 9 cm). We pulled the predator toward the frog beginning at a distance of 150 cm, using the same experimenter to maintain consistency (according to video analysis, approximate pulling rate of 150 cm to 50 cm distance was 12 cm/s, with the final 50 cm slowing to 7 cm/s). A webcam was mounted over the predator arena to film trials for later confirmation of predator approach speed and frog behavioral responses.

To begin, the frog was placed on a short PVC perch elevated and centered within a 1-m diameter circular arena, with an attached runway facing in the direction of the predator. As the predator approached, we scored the following frog behaviors: flinching, turning, hiding, and jumping. We considered behaviors that happened both before and the moment when the predator collided with the perch, although the severity of responses before/after contact was scored differently. If the frog exhibited no jumping response before the predator made contact, the trial was repeated again for a maximum of three attempts to assess the breadth of behavioral responses.

Measure of boldness

Flight initiation distance (FID) is a commonly used measure in studies examining anti-predator behavior. However, it indicates only the endpoint of a response, and we aimed to use a more nuanced measure of escape by including more subtle behaviors. We focused on three behaviors (see above), and assigned them a numerical value ranging from 0 to 1 representative of the severity of the response: flinch at contact = 0.1, flinch before contact = 0.2, turn at contact = 0.3, turn before contact = 0.4, jump/hide at contact = 0.8, and jump/hide before contact = 1.0. We calculated an "escape score" from the sum of the behaviors exhibited by each frog, adjusted by the number of attempts (escape score = \sum anti-predator behaviors/# attempts). For example, a frog that flinched, turned, and jumped all before contact during the first attempt would receive the maximum possible score of 1.6 [(1 + 0.2 + 0.4)/1], and a frog that across three attempts turned once at contact would receive a score of 0.1 [(0.3)/3]. The minimum possible value representing the least severe escape response, reflecting no behavioral responses across three replicates, would be 0 [(0 + 0 + 0)/3]. For a more intuitive measure, we divided the escape response calculation by the maximum possible value [escape response/(1.6)], consequently bolder individuals had higher final escape scores.

Body measures

We measured body length (snout-vent-length = SVL) using a plastic caliper (to the nearest 0.1 mm) and body mass (to the nearest 0.1 g) using an Ohaus CS200 digital scale at various points in the experimental sequence. We estimated body condition using residuals from a regression of post-oviposition mass on SVL. Given the short-term duration of the experiment, SVL was measured only during the phonotaxis trials. Whereas mass was collected on three occasions: 1) after the phonotaxis trials, 2) at the start of the personality trials post-oviposition, and 3) after the conclusion of the personality trials. Mean body weight did not change over the course of the experiment (two-sample *t*-test: $t = 0.55$, $df = 111.7$, $P = 0.58$), suggesting that husbandry was adequate.

Statistical analysis

To test whether frogs show personality (i.e., maintain escape behaviors over time), we used a standard least squares model (REML method). We entered the escape score as the response variable, the experiment replicate as the ordinal predictor variable, and female ID as a nominal random term. Note that for the test of the hypothesis, the important term is female ID since the proportion of total variance that is attributable to individual identity can be used as the estimate for repeatability.

To explore whether escape behaviors were distinct between individuals, we computed the mean and coefficient of variation (CV) across replicates per female. Means represent an overall measure of boldness, whereas CVs represent a measure of consistency. We used pairwise correlations to explore the relationship between mean and CV of escape scores as well as their relationships with body length (SVL) and body condition. The latter was done to ensure that body measures were not a driver of behavioral differences (Maes et al. 2013).

To test whether bolder or more consistent females are choosier, we used a standard least squares model (REML method). We entered choosiness as the response variable, and as predictor variables, we entered mean escape score (as a measure of personality), CV of escape score (as a measure of consistency), as well as SVL and body condition.

To put the effect of personality and consistency on choosiness into context, we also calculated eta-squared (η^2) as a measure of effect size. The η^2 values smaller than 0.13 indicate small effect sizes, values from 0.13 to 0.26 indicate intermediate effect sizes, and values greater than 0.26 indicate large effect sizes (Cohen 1988). At our sample size ($n = 58$), we had adequate power ($\alpha = 0.05$; $1 - \beta = 0.2$) to detect a minimal effect size of $r = 0.36$ (i.e., medium effect size, equivalent to η^2 of 0.13–0.26). All statistical tests were computed in JMP version 13 (SAS Institute, Cary, NC).

RESULTS

Choosiness varies between females

Choosiness was highly variable across females spanning the range of tested values from 0 dB to 24 dB (Figure 1). This indicates that females demonstrated unique baseline degrees of choosiness when in a consistent lab setting devoid of environmental fluctuations.

Evidence of treefrog personality using boldness

Females displayed a strong individual component in boldness when confronted with a simulated predator (Figure 2A,B). The repeatability estimate from the female ID score was significant (95% confidence interval [CI] = 0.04–0.11; Wald's $P < 0.0001$; $r = 0.52$). We also found a significant effect of replicate ($F_{3,171} = 6.36$; $P = 0.0004$). During the first replicate, females were less bold than during the later three replicates (least squares means of escape score = 0.89 vs. 1.06, 1.05, and 1.07, respectively), which we suspect is due to the novelty of being placed in the predator trial setup. However, treating the first replicate as a training trial and removing it from the analysis did not change the significant effect of female ID, so conservatively we included all replicates in the remainder of the analysis.

Using pairwise correlations, we found that neither mean escape score nor the escape score CV were related to body length (SVL) or body condition (in all cases $r < |0.17|$; $P > 0.21$). However, personality and consistency were significantly

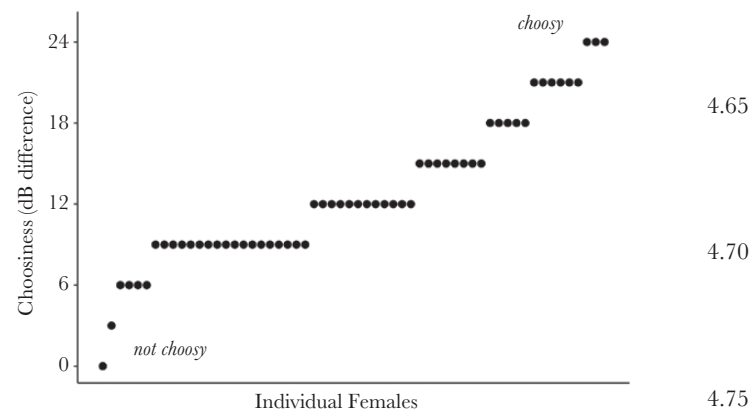


Figure 1

Choosiness, scored as the highest amplitude difference (in dB) at which the female still approaches the attractive call, is highly variable across females. Females are arranged from lowest to highest choosiness; greater decibel difference indicates a choosier female.

correlated: bolder individuals were more consistent ($r = -0.71$; $P < 0.0001$; Figure 2C).

More consistent females are choosier

Choosiness was significantly related to consistency (escape score CV), although the effect size was of small magnitude ($\eta^2 = 0.09$; Table 1; Figure 3B). This suggests that consistently bold frogs are choosier when searching for prospective mates. Choosiness was not significantly related to average personality (mean escape score) (Figure 3A) nor to body measures (Table 1).

Table 1

Results of a LSM model showing the relationship between choosiness and different modifying variables

Source	df	F	P	η^2
Mean Escape score	1,57	0.62	0.43	0.01
CV Escape score	1,57	5.77	0.02*	0.09
Body length (SVL)	1,57	0.71	0.40	0.01
Condition	1,57	3.18	0.08	0.05

Significant effect indicated by asterisk.

Eta-squared (η^2) as a measure of effect size; η^2 values < 0.13 indicate small effect sizes, values from 0.13 to 0.26 indicate intermediate effect sizes, and > 0.26 indicate large effect size.

DISCUSSION

This study explored whether personality is present in adult gray treefrogs, and whether it may explain individual variation in mate choice decisions. We found evidence of personality and that consistently bold females were choosier. Our assay for choosiness simulates a female's willingness to travel further distances to reach a more attractive mate. In nature, that would translate into choosier females running a higher risk of encountering predators while approaching a male, a challenge best confronted by more consistently bold females.

Mate choice decisions arise from several components, among them mate preferences and choosiness. Mate preferences relate variation in the attractiveness of the sexual ornaments of prospective mates to variation in the features of those ornaments, whereas choosiness

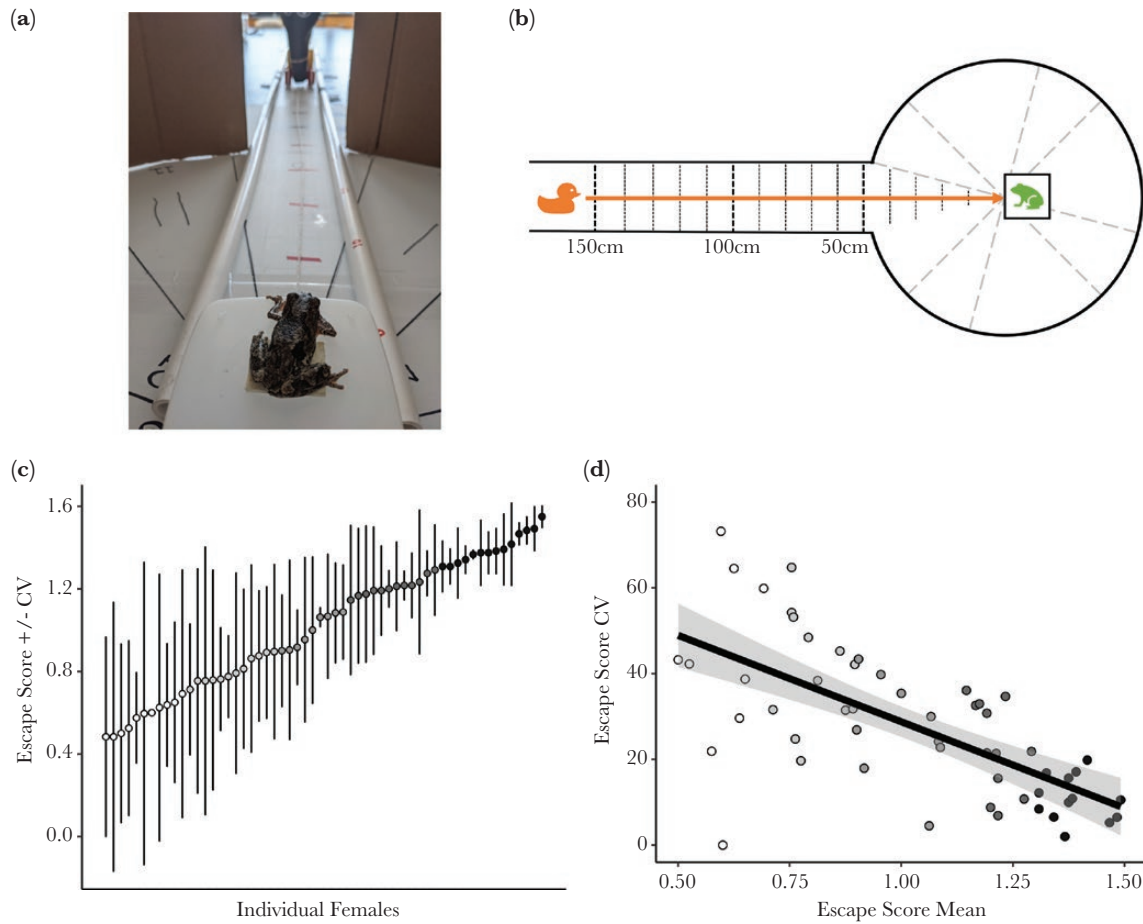


Figure 2

Panel A visualizes the predator approach assay used to measure boldness by recording evasive behaviors (flinches, turns, jumps) as the frog’s response to stimulated predator threat. This assay generates escape scores and shows repeatable variation among females (evidence of personality). Panel B shows the approaching predator from the perspective of a frog. Panel C shows each female’s individual mean escape scores (relative personality phenotype), ranked by increasing boldness, with the within-individual CV expressed as percentage. Panel D shows that bolder females (high mean escape score) were also more consistent (low escape score CV). In Panels C and D, the symbol color denotes degree of boldness (darker = bolder) in five steps (increase of 0.2 per step; range 0.5–1.5).

describes the effort an individual is willing to expend to acquire the preferred mate type (Jennions and Petrie 1997; Neelon et al. 2019; Feagles and Höbel 2022b). These components vary independently from each other, and each component is likely influenced by different factors or in different ways by the same factor (Neelon et al. 2019; Feagles and Höbel 2022b). In a previous study, Feagles and Höbel (2022b) examined the effects of hormones, body measures, and reproductive investment on preferences and choosiness in female gray treefrogs. They found that variation in choosiness was related to variation in sex and stress hormone levels (large effect sizes $\eta^2 = 0.28$ and 0.35 , respectively), while variation in some preference function traits was related to differences in body size and condition (effect sizes ranged from small to large: $\eta^2 = 0-0.39$). By comparison, effect sizes of personality traits determined here were only of small magnitude, suggesting that personality plays a statistically significant yet comparatively minor role in determining variation in choosiness in this species. However, because preferences and choosiness are influenced by different factors in this species (Feagles and Höbel 2022b), having found a weak effect of boldness on choosiness for longer duration calls does not imply that choosiness could not be influenced by other personality traits such as activity or aggressiveness, nor that boldness

could not show a completely different relationship (i.e., stronger, reversed pattern) with call duration preferences.

The majority of prior studies examining personality in the context of mate choice focus on whether there are preferences for certain personality types (Wang et al. 2022), whether there is assortative mating based on personality type (i.e., Kralj-Fiser et al. 2013; Pogány et al. 2018; Collins et al. 2019), or whether there are fitness benefits arising from such assortative mating (i.e., Both et al. 2005; Schuett et al. 2011; Rangassamy et al. 2015). Studies examining how a chooser’s personality type may affect mate choice decisions for attractive phenotypic traits, as in the present study, are still rare. In mosquitofish, male personality was not associated with mate preferences for larger female body size and size-assortative mating (Li et al. 2022). However, in shortfin mollies, bold/explorative females showed stronger preferences for conspecific over heterospecific males, and more explorative females preferred smaller conspecific males (Sommer-Trembo et al. 2016; Li et al. 2022). Echoing our results, the effect sizes of these personality–mate preference relationships were of small magnitude (in all cases, $r < 0.24$).

Given the small sample of tested species, it is premature to conclude that personality type could not be a strong predictor of

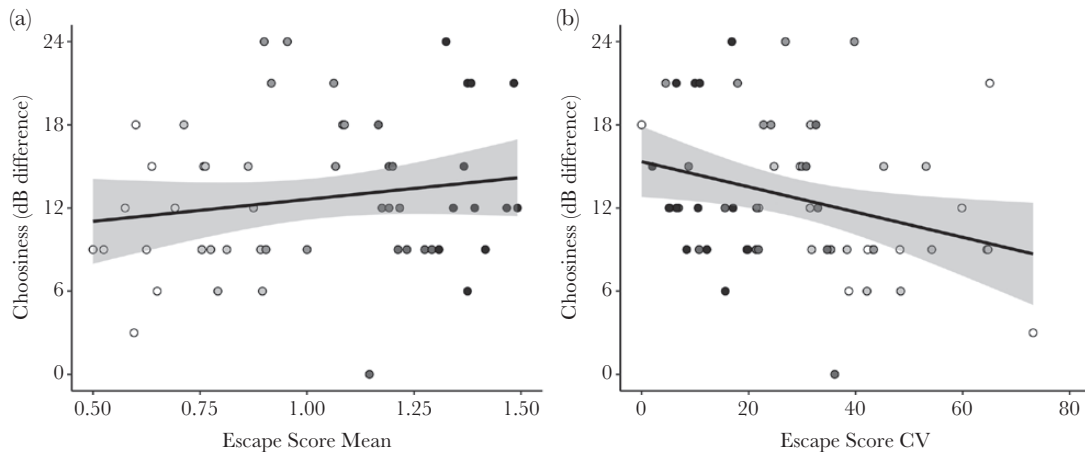


Figure 3

Relationship between personality and choosiness. Panel A shows there was no relationship between the personality phenotype (mean boldness) and choosiness (highest amplitude difference in which the female chose the attractive stimulus). Panel B shows there was a significant, negative correlation between consistency in escape responses (CV) and choosiness: individuals that are more consistent in their escape responses were choosier. In both panels, symbol color denotes degree of boldness (darker = bolder) in 5 steps (increase of 0.2 per step; range 0.5–1.5).

preferences and/or choosiness. Animal personality can vary across several axes (boldness, exploration, activity, sociability, aggressiveness) (Réale et al. 2007), and perhaps a link between mate choice decisions and personality requires a suite of correlated personality traits (i.e., behavioral syndromes) to manifest (but see Li et al. 2022 who found evidence for behavioral syndromes but no correlation with preference). More empirical data will be required to explore the extent to which personality makes a contribution to final mating decisions, and consequently on patterns of sexual selection.

FUNDING

This work was supported by the Ruth I. Walker and Raymond E. Hatcher Memorial Scholarships and the University of Wisconsin Milwaukee's Graduate Student Excellence Fellowship for financial support of O.S.F.

We thank K. Stratman, G. Augusto-Alves, J. Cannizzaro, and H. Warner for help with fieldwork and data collection and R. Rodríguez, P. Dunn, L. Whittingham, and E. Latch for feedback on the project. We also thank the staff at the University of Wisconsin Milwaukee's Field Station for access to research facilities.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Olivia Feagles (Conceptualization [Equal], Data curation [Lead], Formal analysis [Equal], Funding acquisition [Lead], Investigation [Lead], Methodology [Equal], Resources [Equal], Visualization [Equal], Writing – original draft [Lead], Writing – review & editing [Equal]), and Gerlinde Höbel (Conceptualization [Equal], Data curation [Supporting], Formal analysis [Equal], Funding acquisition [Supporting], Investigation [Supporting], Methodology [Equal], Resources [Equal], Supervision [Lead], Visualization [Equal], Writing – original draft [Equal], Writing – review & editing [Equal])

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Feagles and Höbel (2023).

Handling Editor: Aliza le Roux

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