PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Höbel G, Rodríguez RL. 2022 Positive-to-negative behavioural responses suggest hedonic evaluation in treefrog mate choice. *Proc. R. Soc. B* **289**: 20211822.
https://doi.org/10.1098/rspb.2021.1822

Received: 16 August 2021
Accepted: 16 December 2021

Subject Category:
Evolution

Subject Areas:
evolution

Keywords:
aversion, hedonic evaluation, Hylidae, mate choice, sexual selection

Author for correspondence:
Gerlinde Höbel
e-mail: hoebel@uwm.edu

Positive-to-negative behavioural responses suggest hedonic evaluation in treefrog mate choice

Gerlinde Höbel and Rafael L. Rodríguez

Behavioral and Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin–Milwaukee, Milwaukee, WI 53201, USA

GH, 0000-0003-0786-7734

Sexual competition hinges on the ability to impress other conspecifics, to drive them away or attract them. In such cases, the selective environment may be hedonic or affective in nature, as it consists of the evaluations of the individuals making the decisions. This may contribute to the power of sexual selection because evaluations may range from positive to negative rather than simply from positive to neutral. Selection due to mate choice may therefore be stronger than currently appreciated. Further, change in preferred mate types can occur simply by changes (flips) in the evaluation of similar display features, adding to the dynamism of sexual selection as well as its strength. We tested the hypothesis of positive-to-negative behavioural responses in mate choice with a playback experiment using two treefrog species with ‘mirror image’ structures in their advertisement and aggressive calls. Female treefrog responses ranged from approach to evasion, and the presence of an aversive stimulus tainted evaluation of an attractive stimulus. Further, females in the two species showed flips in approach/evasion of stimuli with comparable signal structure. These results suggest that hedonic evaluation may have an important role in mate choice and showcase how mechanistic analysis can help understand evolutionary processes.

1. Introduction

One of the more remarkable aspects of the natural world is the sheer number and diversity of life forms that have arisen along the history of Earth [1]. And one of the more remarkable aspects of this diversity is the extent to which it is due to evolution under sexual selection [2–5]. How natural and sexual selection interact in the generation of diversity remains to be fully understood [6,7]. It is clear, however, that sexually selected traits are very often the most divergent aspects of the phenotypes of closely related species (e.g. [8–12]), as well as being the most extravagant and showy traits in nature (e.g. [4,13,14]).

Sexual selection can generate extraordinary diversity because of the special nature of sexual competition. Sexual selection is stronger and more constant year-to-year than natural selection [3,9,15–18]. Further, success in sexual competition often hinges on the ability to impress other conspecifics, either to drive them away (competitors) or attract them (potential mates), rather than on the ability to forage and survive. In mate choice, for instance, the selective environment may be hedonic in nature (i.e. involving positive or negative affective states—emotions and desires), as it consists of the evaluations of the individuals making the decisions [2,19–24]. The broad basis for this study is the hypothesis of hedonic evaluation in mate choice. This hypothesis states that, although courtship displays must function well in their physical and ecological contexts [6,25], they are mainly under selection due to mate choice decisions regulated by affective-emotional mechanisms.

But why would hedonic evaluation contribute to the power of sexual selection due to mate choice? One reason is that hedonic valences range from positive to negative [22,24]—the distance between ‘beautiful’ and ‘repulsive’ is greater

THE ROYAL SOCIETY
PUBLISHING

than the distance between merely attractive and unattractive. The response to courtship displays may thus range not only from attractive to unattractive but attraction to avoidance. Consequently, selection due to the expression of mate preferences [26] may be stronger than currently appreciated. Another reason is that evolutionary change in preferred mate types may often not require complex 're-wiring' of the underlying neural mechanisms, but involve instead simpler switches in the valence assigned to the same display feature—species divergence in mate preferences may involve 'flips' in whether a given stimulus is assigned positive or negative valences [22,23]. This may add to the speed of evolution under sexual selection. Understanding the evolutionary consequences of mate choice may therefore require analysing the hedonic nature of the mechanisms that regulate mate choice, and assessing how widespread such mechanisms are in nature.

Here, we focus on the behavioural aspects of the hypothesis of hedonic evaluation in the process of mate choice with two species of *Hyla* treefrog (Anura: Hylidae). We tested two predictions. First, female treefrogs evaluating male signals should express responses that range from positive to negative—from attraction to avoidance [22,23]. Further, with a positive–negative range of evaluation, the presence of an aversive stimulus may influence the evaluation of an otherwise attractive stimulus—reducing its attractiveness or even switching it to now be aversive, as if the whole context or setting became 'tainted'. We therefore also asked whether responses depended on the presence of an aversive stimulus near an attractive stimulus, and whether varying the features of the former made a difference for this effect.

The second prediction pertains to flips in the evaluation of similar display features—which are not required by the hedonic hypothesis but are countenanced by it. Such flips should be reflected in attraction/avoidance behaviours [22,23]. To address this possibility, we took advantage of the natural call repertoire of male treefrogs. In the North American treefrogs, advertisement calls (aimed mainly at females) in one clade are structured like aggressive calls (aimed at males) in a different clade, and vice versa, with the presence/absence of amplitude modulation defining either call type (figure 1). This contrast in the structure of the different call types permits asking whether the evaluation of comparable call features is flipped across species.

2. Methods

(a) Study species and sites

We worked with *Hyla cinerea* green treefrogs and *H. versicolor* eastern grey treefrogs. *Hyla cinerea* is a common species found throughout the southeastern USA [28], and we collected females and conducted choice trials at the Texas Freshwater Conservation Center (TFCC) in Jasper County, Texas. *Hyla versicolor* is a common species found throughout the northeastern USA [28], and we collected females from a pond adjacent to the UWM Field Station, Ozaukee County, Wisconsin, and conducted female choice trials at the University of Wisconsin–Milwaukee (UWM).

We obtained females by collecting pairs in amplexus around the peak of male calling activity (21.00–23.00 h). This assured that females were sexually responsive, and that they had not yet laid eggs, after which they become unresponsive to playback stimuli. We tested females within 2 days of being collected and subsequently released them at the capture ponds.

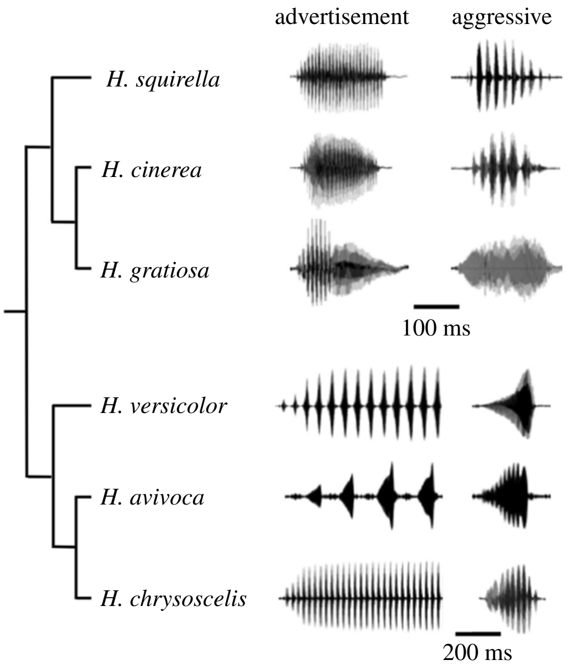

Figure 1. Sonograms of advertisement and aggressive calls of the focal species *Hyla cinerea* (green treefrog) and *H. versicolor* (eastern grey treefrog), together with calls of their closest relatives. Notice differences in amplitude modulation depth (long pulse versus train) between advertisement and aggressive call within clades. Phylogeny follows [27]; call recordings obtained by G. Höbel, B. Buchanan (*H. squirella* aggr. call), C. Murphy (*H. gratiosa* aggr. call), C. Martinez (*H. avivoca* calls) and C. Gerhardt (*H. chrysoscelis* calls).

(b) Do female treefrogs express a positive–negative range of responses when evaluating male signals?

We conducted single-speaker acoustic playback trials that presented female treefrogs singly with their conspecific advertisement call and their conspecific aggressive calls, in random order. We observed the reaction of the females to the playbacks and scored their behaviour on a five-point scale ranging from attraction to avoidance (see '*Scoring female behaviour*' below). Sample size for single-speaker trials was $n = 20$ females per trial.

To ask whether the presence of an aggressive call influences the evaluation of an advertisement call, we conducted two-choice trials that presented the conspecific advertisement call alongside the conspecific aggressive call. We scored the reaction of the females on the five-point scale ranging from attraction to avoidance (see '*Scoring female behaviour*' below). We conducted a total of four two-choice trials for each species. In one trial, the stimuli had the mean features of the advertisement and aggressive call of the respective species. In three additional trials, the stimuli were the mean advertisement call of each species against modified aggressive calls, making them either longer, with a faster call rate, or with a lower dominant frequency than the mean aggressive call for each species (which also made the modified aggressive calls longer, or faster or lower in frequency than the mean advertisement calls for each species) (table 1). Changing these features in advertisement calls in these ways (longer, faster and lower) would make them more attractive [29–32]. Consequently we wanted to ask whether longer, faster or lower aggressive calls would be less aversive than the average aggressive call and thus have less of a negative influence on the evaluation of the otherwise attractive advertisement call. We randomized the order of these trials, and the loudspeaker from which each stimulus was broadcast, across females. Sample size for choice trials was $n = 20$ females per trial.

Table 1. Parameters of stimuli used in playback trials of advertisement and aggressive calls to *Hyla cinerea* and *H. versicolor* females. Average advertisement and aggressive stimuli are based on mean values found in the respective study populations. Additional aggressive call stimuli represent longer, faster and lower frequency alternatives. In two-choice trials with equal call period (mean, longer, lower), stimuli were broadcast perfectly alternating with each other; in trials where one alternative was presented at a faster rate, we adjusted stimuli to avoid overlap.

		mean call features	aggressive longer	aggressive with faster rate	aggressive with lower frequency
H. cinerea	advertisement stimulus	125 ms 900 + 2700 Hz 550 ms period			
	aggressive stimulus	125 ms (5 pulses) 900 + 2700 Hz 550 ms period	150 ms (6 pulses) 900 + 2700 Hz 550 ms period	125 ms (5 pulses) 900 + 2700 Hz 350 ms period	125 ms (5 pulses) 800 + 2400 Hz 550 ms period
H. versicolor	advertisement stimulus	900 ms (18 pulses) 1100 + 2200 Hz 5000 ms period			
	aggressive stimulus	920 ms (3 calls; 160 ms call + 220 ms silence)[a] 1100 + 2200 Hz 5000 ms period	1050 ms (3 calls @ 210 ms) 1100 + 2200 Hz 5000 ms period	920 ms (3 calls @ 160 ms) 1100 + 2200 Hz 2500 ms period	920 ms (3 calls @ 160 ms) 900 + 1800 Hz 5000 ms period

[a] *H. versicolor* aggressive calls are mostly given in short series, not as single calls. We therefore presented aggressive calls in a series of three calls, which also resulted in the entire stimulus having roughly the same total length as the advertisement call.

(c) Are there species differences (flips) in the evaluation of comparable signal features?

In our two study species, the advertisement call in one species is structured like the aggressive call in the other species, and vice versa (figure 1). In green treefrogs, *H. cinerea*, the advertisement call is a single long pulse without amplitude modulation, while the aggressive call is heavily amplitude-modulated, giving it a pulsed structure. Eastern grey treefrogs, *H. versicolor*, by contrast, have an advertisement call composed of a train of short pulses, while the aggressive call is one long pulse. Thus, there should be corresponding flips in signal evaluation: female green treefrogs should find attractive precisely the structure that female grey treefrogs avoid and vice versa.

(d) Stimulus generation

We synthesized acoustic stimuli in R (v. 3.1.0) software [33], using the seewave [34] and TuneR [35] packages. For two-choice trials, we used Audacity software (v. 2.02, http://audacity.sourceforge.net/) to generate stereo files and to adjust the relative timing of the stimuli. We presented the playbacks from JBL Control 1Xtreme loudspeakers. We set the amplitude of all playbacks to 85 dB SPL at the female's release point (1 m from the loudspeakers) using a sound pressure level meter (Extech 407764; fast RMS,'C' weighting).

(e) Test procedure

We tested females in a circular playback arena (2 m diameter). The floor of the arena were exercise mats (EVA foam interlocking mats), the walls were 50 cm high wire mesh panels covered in lightweight black cloth (acoustically transparent but visually opaque). The speakers were placed 90 degrees apart just outside the arena facing the arena centre. A 20 × 10 cm 'choice zone' in front of the speaker was demarcated using tape placed on the floor of the arena. The tape marks were necessary because both frog and observer could not see the speakers that were hidden behind the cloth screen of the arena. For testing, females were placed in an acoustically transparent release cage at a distance of 1 m from each of the playback speaker(s). After five call repetitions, we lifted the lid of the release cage by pulling a string and the female was allowed to move freely about the arena.

For *H. cinerea*, the arena was set up inside a large wooden shed at TFCC in Texas. Background noise levels were 50–55 dB SPL. Female movements were monitored visually with illumination provided by a dim red bulb light mounted above the arena's centre (1.2 lux). For *H. versicolor*, the arena was set up inside a semi-anechoic room at UWM. Dim illumination mimicking overcast night sky was provided by a GE 55507 night-light mounted above the arena. Female movements were monitored remotely via an IR sensitive camera and IR light sources mounted on the room ceiling.

(f) Scoring female behaviour

We observed female behaviour towards the playback stimuli and scored behavioural responses ranging from approach to active avoidance (table 2). For the two avoidance responses, we also noted the direction in which the females attempted to leave (the angle relative to a 'focal' speaker). In single-speaker trials, we set the speaker's location as 0 degrees and expressed the leave angle in a clockwise direction. In two-choice trials, we set the focal speaker as the one broadcasting the advertisement stimulus (set as 0 degrees) and expressed the leave angle relative to the direction in which the aggressive call was broadcast (at 90 degrees); we periodically changed speaker directions to guard against side bias.

(g) Statistical analysis

For the tests detailed below, we fit linear mixed models in JMP (15.2.1). We presented most females with more than one stimulus in the playback trails (all females of both species with both stimuli in the single-speaker trials; all *H. versicolor* females and most *H. cinerea* females with all or some of the stimuli in the two-speaker trials). We therefore included female identity as a random term in all the models below.

Table 2. Response scores and the female behaviours associated with them.

+1	+0.5	0	−0.5	−1
attraction	**slight attraction**	**indifference**	**slight avoidance**	**avoidance**
female deliberately approaches and enters choice zone in front of a speaker	initial approach towards a speaker that is subsequently aborted & female remains inside testing arena	female either does not leave release box, or wandered aimlessly around the arena for the duration of the 5 min trials period	initial approach towards a speaker that is subsequently aborted & female deliberately climbs up arena wall attempting to leave	female deliberately climbs up arena wall attempting to leave without having previously approached a speaker

(i) Do female treefrogs express a positive–negative range of responses when evaluating male signals?

To analyse the single-speaker trials, we used a model with female response score as the dependent variable. The explanatory variables were species, stimulus type (advertisement versus aggressive for each species) and the species × stimulus type interaction. The species term tests for species differences in overall evaluation of the stimuli; the stimulus type term tests for differences in overall evaluation of the call types; and the interaction term tests for species differences in evaluation. The female identity random term adjusts the degrees of freedom to prevent pseudoreplication and tests for individual differences in overall evaluation.

(ii) Does the presence of an aggressive call influence evaluation?

To analyse the two-speaker trials, we used a model with female response score as the dependent variable. The explanatory variables were species, the features of the aggressive call that was contrasted with the advertisement call (mean features, longer, with faster rate, with lower frequency), and the species × aggressive call feature interaction. The species term tests for species differences in overall evaluation of the stimuli; the aggressive call feature term test for an effect of these features on overall evaluation; and the interaction term tests for species differences in that effect. The female identity random term adjusts the degrees of freedom to prevent pseudoreplication and tests for individual differences in overall evaluation.

(iii) Are there species differences (flips) in the evaluation of comparable signal features?

Because of the differences in the structure of advertisement and aggressive calls between *H. versicolor* and *H. cinerea* (see above), the interaction terms in the above models test for flips in evaluation between the two species.

3. Results

(a) Female treefrogs express a positive–negative range of responses when evaluating male signals

In single-speaker trials, 100% of 20 females in each species approached the advertisement call, but there was much more variation in the response to the aggressive call (figure 2*a*). Response scores were correspondingly 100% positive versus 0 to negative on average (figure 2*b*; significant stimulus type term in table 3). The species and species × stimulus types were marginally significant (table 3), hinting at somewhat more negative evaluations of aggressive calls in *H. cinerea*. There was no detectable individual variation in these patterns (non-significant random term in table 3).

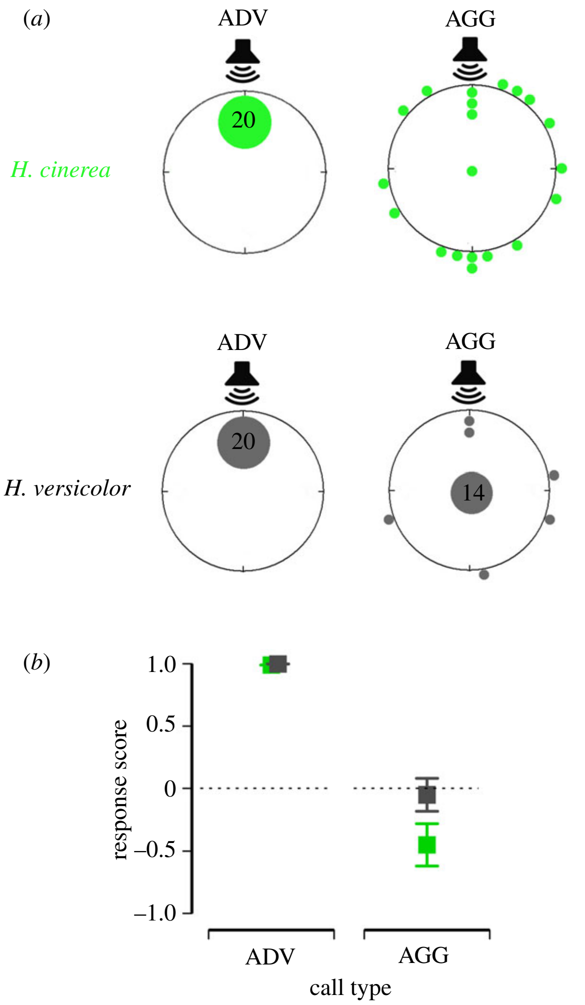

Figure 2. Responses of female treefrogs to single-speaker trials presenting either the conspecific advertisement (ADV) or aggressive (AGG) call. (*a*) When hearing the conspecific advertisement call, all females of both species approached it. When hearing the conspecific aggressive call, females showed a range of responses, from attraction (symbols inside the arena in front of the speaker symbol), indifference (symbols in centre of arena) to avoidance (symbols outside the arena border indicating their escape route). Unless otherwise indicated, one symbol represents the response of one female. (*b*) Average response scores were positive in response to advertisement calls, but neutral to negative in response to aggressive calls. Responses of *H. cinerea* are shown in green; responses of *H. versicolor* are shown in grey. (Online version in colour.)

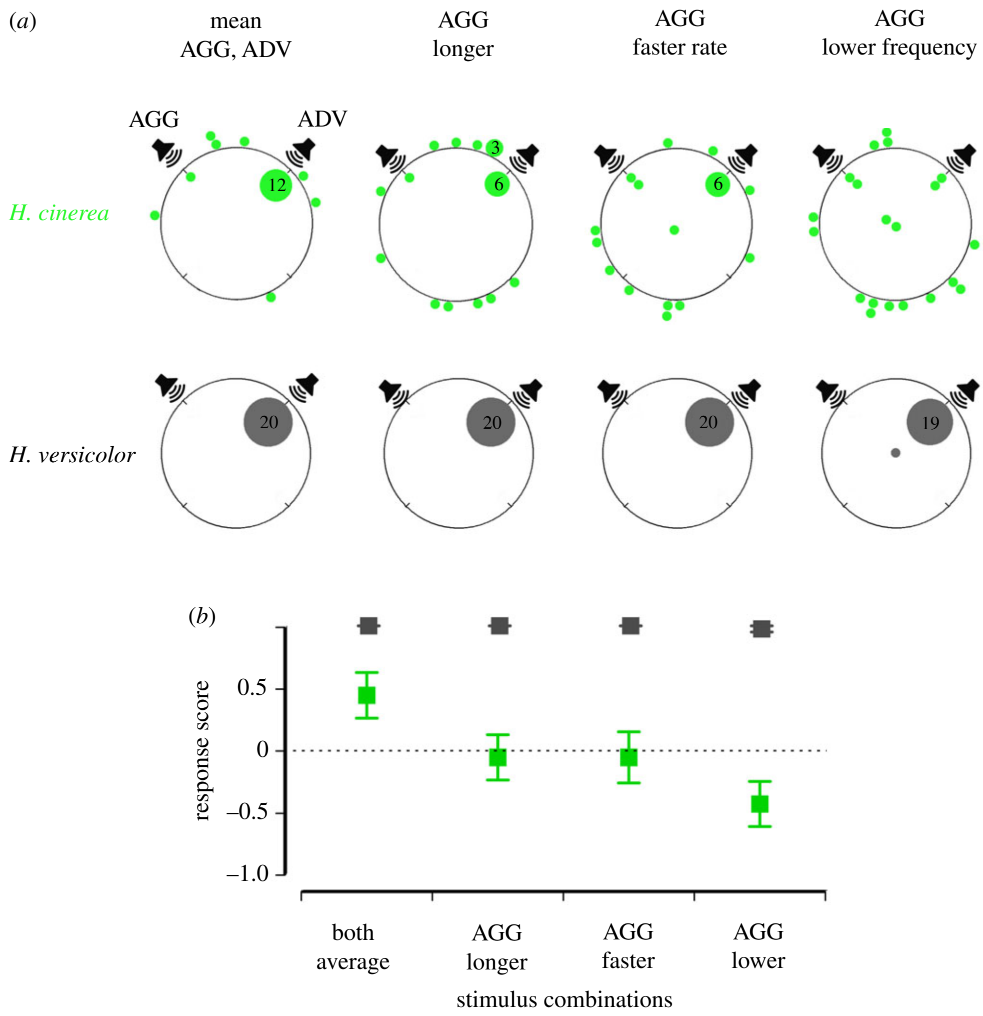

Figure 3. Responses of female treefrogs to two-choice trials presenting the conspecific advertisement (ADV) call together with the aggressive (AGG) call. (*a*) The majority of *H. versicolor* females approach the advertisement call regardless of the presence and features of the aggressive call; by contrast, some *H. cinerea* females approach the advertisement call, a few even approached the aggressive call, and many sought to leave the arena or showed no response. Symbol position indicates female response, and unless otherwise indicated, one symbol represents the response of one female. (*b*) Average response scores were across the board positive for *H. versicolor*. By contrast, average scores for *H. cinerea* ranged from somewhat positive (0.5) to somewhat negative (−0.5). Responses of *H. cinerea* are shown in green; responses of *H. versicolor* are shown in grey. (Online version in colour.)

Table 3. Analysis of variation in the response of *Hyla cinerea* and *H. versicolor* to the single-speaker trials presenting each species advertisement and aggressive calls. We show the output of the linear mixed model (see Statistical analysis): *F*-ratio tests for the fixed terms and the 95% confidence interval (CI) and Wald *p*-value for the random term.

term	d.f. num, den	*F*	*p*
species	1, 38	3.49	0.069
call type	1, 38	136.49	<0.0001
species × call type	1, 38	3.49	0.069
individual ID		95% CI	Wald *p*
		−0.037–0.073	1.0

(b) The presence of an aggressive call influences evaluation differently in different species

In two-speaker trials, 95–100% of 20 *H. versicolor* females approached the advertisement call regardless of the presence and features of the aggressive call (figure 3*a*). By contrast, only 10–60% of 20 *H. cinerea* females approached the advertisement call, with 35–70% of females seeking to leave the arena, 0–10% showing no response and 5–10% approaching the aggressive call (figure 3*a* and figure 4). Accordingly, response scores for *H. versicolor* were 95–100% positive across all trials, but ranged from 1 to −1 for *H. cinerea*, averaging *ca* 0.5 to −0.5 (figure 3*b*). Thus, there was an overall species difference in evaluation (significant species term in table 4), an overall effect of the presence and features of the aggressive call (significant aggressive call features term table 4), and a species difference in that effect (significant interaction term in table 4). Interestingly, modifying the features of the aggressive call in ways that make advertisement calls more attractive either had no effect on evaluation (*H. versicolor*) or made evaluation even more negative (*H. cinerea*) (figure 3*b*; table 4). There was also no detectable individual variation in these patterns (non-significant random term in table 4).

(c) Flips in the evaluation of comparable signal features

The call structures given positive and negative evaluations were flipped between the two treefrog species—each species' attractive call structure (with/without amplitude modulation) was aversive to the other, with a species difference in the strength of avoidance (figure 2).

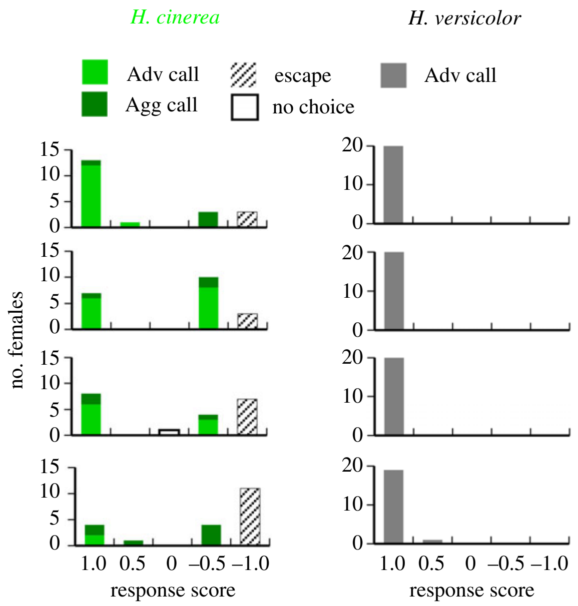

Figure 4. Responses of female treefrogs to two-choice trials presenting the conspecific advertisement (Adv) call together with aggressive (Agg) calls (mean, longer, faster, with lower frequency). *Hyla cinerea* females showed a wide range of evaluations, including attraction to both the advertisement and aggressive call as well as avoidance. By contrast, for *H. versicolor* the presence of aggressive calls did not influence their positive evaluation of the advertisement call. (Online version in colour.)

Table 4. Analysis of variation in the response of *Hyla cinerea* and *H. versicolor* to the two-speaker trials presenting each species advertisement call together with their aggressive calls modified in various ways. We show the output of the linear mixed model (see Statistical analysis): *F*-ratio tests for the fixed terms and the 95% confidence interval (CI) and Wald *p*-value for the random term.

term	d.f. num, den	*F*	*p*
species	1, 32.7	161.3	<0.0001
aggressive call features	3, 110	3.61	0.016
species × aggressive call features	3, 110	3.27	0.024
		95% CI	Wald *p*
individual ID		−0.081–0.009	1.0

4. Discussion

We report that females in two treefrog species expressed responses that ranged from positive to negative when evaluating male calls, from deliberate approach to deliberate avoidance. For one of the two species, the presence of the aversive stimulus influenced the context of evaluation of an otherwise attractive stimulus, with the whole context becoming ‘tainted’. Varying the features of the aversive stimulus in ways that make the attractive stimulus more attractive did not reduce this effect, but instead exacerbated it. Finally, as the two treefrog species show reversed structure of their advertisement and aggressive calls (in what constitutes one call type or the other), we also found evidence of flips in the evaluation between the species: comparable signal structures were respectively attractive or aversive.

These results may help explain the greater strength and constancy of sexual selection compared with natural selection [3,9,15–18]. As evaluations and behavioural responses range from positive to negative [22,24], the distance between peak attractiveness and peak aversion may be greater than without such evaluation, adding to the strength of selection due to the expression of mate preferences. Another distinctive feature of sexual selection is its greater dynamism, producing faster divergence. Flips in whether comparable signal features are given positive or negative evaluations may add to the speed of change in preferred/aversive mate types [22,23]. This is an example of how evolutionary insight may be gained by analysis of the mechanisms of decision making that regulate animal behaviour [36].

In this study, we interpret evasion of contexts containing aggressive calls in terms of the evaluation. A related possibility, however, is that the frogs’ behaviour may represent adaptive avoidance of situations where aggression may be about to ensue, not necessarily signifying negative evaluation. We do not consider this likely, however, because physical combat between male frogs in these species, which involves grappling, wrestling or kicking, may on occasion be exhausting for the involved males, but does not result in injury, except in very few species where males have weapons such as spines or fangs [37]. The species studied here do not possess weapons, and fights are generally brief and non-injurious ([38]; G. Höbel 2017, pers. obs.).

We note that our results are consistent with the hypothesis of hedonic (i.e. affective) evaluation in mate choice [22,23]. Its relevance in mate choice, with its potential contributions to the strength and speed of evolution under sexual selection [22–24], depends on how widespread it is among different animals. Comparative research will be required to answer the twin questions of whether mate choice involves responses ranging from the positive to the negative, and whether those responses follow from hedonic valences that range from attraction to revulsion. Attention to behavioural detail will be highly illuminative.

Ethics. Frogs were collected with permission from local landowners and with permits obtained from local Departments of Natural Resources (permit no. SPR-0507-892, licence no. SRLN-21-19). Experimental procedures were approved by the Animal Care and Use Committee of the University of Wisconsin–Milwaukee (protocol no. 17-18#01).

Data accessibility. Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.41ns1rndz [39].

Authors’ contributions. G.H.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft and writing—review and editing; R.L.R.: conceptualization, formal analysis, visualization, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. The authors declare no competing interests.

Funding. Fieldwork was supported by UWM Research Growth Initiative (RGI) and UWM Research and Creative Activities Support (RACAS) grant to G.H. During the preparation of this manuscript, R.L.R. was partially supported by NSF IOS-1855962 to R.L.R. and C.D., and by a UWM Discovery and Innovation (DIG) grant.

Acknowledgements. We thank the staff at the East Texas Conservation Center and the UWM Field Station for logistical support, T. Mendelson and T. Price for productive discussions and encouragement, and N. and M. Byers for access to their property. We are also grateful to Locke Rowe and two anonymous reviewers for constructive comments to the manuscript.

References

1. May RM. 1992 How many species inhabit the Earth? *Sci. Am.* **267**, 42–49. (doi:10.1038/scientificamerican1092-42)
2. Darwin C. 1871 *The descent of man, and selection in relation to sex*. London, UK: J. Murray.
3. West-Eberhard MJ. 1983 Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**, 155–183. (doi:10.1086/413215)
4. Andersson M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
5. Coyne JA, Orr HA. 2004 *Speciation*. Sunderland, MA: Sinauer Assocaites.
6. Safran RJ, Scordato ESC, Symes LB, Rodríguez RL, Mendelson TC. 2013 Contributions of natural and sexual selection to the evolution of premating reproductive isolation: a research agenda. *Trends Ecol. Evol.* **28**, 643–650. (doi:10.1016/j.tree.2013.08.004)
7. Kopp M *et al.* 2018 Mechanisms of assortative mating in speciation: connecting theory and empirical research. *Am. Nat.* **191**, 1–20. (doi:10.1086/694889)
8. Mendelson TC, Shaw KL. 2005 Rapid speciation in an arthropod. *Nature* **433**, 375–376. (doi:10.1038/433375a)
9. Svensson EI, Eroukhmanoff F, Friberg M. 2006 Effects of natural and sexual selection on adaptive population divergence and premating isolation in a damselfly. *Evolution* **60**, 1242–1253. (doi:10.1111/j.0014-3820.2006.tb01202.x)
10. Boul KE, Funk WC, Darst CR, Cannatella DC, Ryan MJ. 2007 Sexual selection drives speciation in an Amazonian frog. *Proc. R. Soc. B* **274**, 399–406. (doi:10.1098/rspb.2006.3736)
11. Safran R *et al.* 2012 A robust new metric of phenotypic distance to estimate and compare multiple trait differences among populations. *Curr. Zool.* **58**, 426–439. (doi:10.1093/czoolo/58.3.426)
12. Seddon N *et al.* 2013 Sexual selection accelerates signal evolution during speciation in birds. *Proc. R. Soc. B* **280**, 20131065. (doi:10.1098/rspb.2013.1065)
13. Eberhard WG. 1985 *Sexual selection and animal genitalia*. Cambridge, UK: Harvard University Press.
14. Emlen DJ. 2014 *Animal weapons*. New York: NY: Henry Holt and Company.
15. Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hoang A, Hill CE, Beerli P, Kingsolver JG. 2001 Strength and tempo or directional selection in the wild. *Proc. Natl Acad. Sci. USA* **98**, 9157–9160. (doi:10.1073/pnas.161281098)
16. Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P, Beerli P. 2001 The strength of phenotypic selection in natural populations. *Am. Nat.* **157**, 245–261. (doi:10.1086/319193)
17. Hereford J, Hansen TF, Houle D. 2004 Comparing strengths of directional selection: how strong is strong? *Evolution* **58**, 2133–2143. (doi:10.1111/j.0014-3820.2004.tb01592.x)
18. Siepielski AM, DiBattista JD, Evans JA, Carlson SM. 2011 Differences in the temporal dynamics of phenotypic selection among fitness components in the wild. *Proc. R. Soc. B* **278**, 1572–1580. (doi:10.1098/rspb.2010.1973)
19. West-Eberhard MJ. 2014 Darwin's forgotten idea: the social essence of sexual selection. *Neurosci. Biobehav. Rev.* **46**, 501–508. (doi:10.1016/j.neubiorev.2014.06.015)
20. Prum RO. 2012 Aesthetic evolution by mate choice: Darwin's really dangerous idea. *Phil. Trans. R. Soc. B* **367**, 2253–2265. (doi:10.1098/rstb.2011.0285)
21. Prum RO. 2017 *The evolution of beauty*. New York, NY: Doubleday.
22. Rosenthal GG. 2017 *Mate choice*. Princeton, NJ: Princeton University Press.
23. Rosenthal GG. 2018 Evaluation and hedonic value in mate choice. *Curr. Zool.* **64**, 485–492. (doi:10.1093/cz/zoy054)
24. Rodríguez RL. 2020 Back to the basics of mate choice: the evolutionary importance of Darwin's sense of beauty. *Q. Rev. Biol.* **95**, 289–309. (doi:10.1086/711781)
25. Endler JA. 1992 Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**, S125–S153. (doi:10.1086/285308)
26. Kilmer JT, Fowler-Finn KD, Gray DA, Höbel G, Rebar D, Reichert MS, Rodríguez RL. 2017 Describing mate preference functions and other function-valued traits. *J. Evol. Biol.* **30**, 1658–1673. (doi:10.1111/jeb.13122)
27. Wiens JJ, Kuczynski CA, Hua X, Moen DS. 2010 An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. *Mol. Phylogenet. Evol.* **55**, 871–882. (doi:10.1016/j.ympev.2010.03.013)
28. Conant R, Collins JT. 1998 *A field guide to reptiles & amphibians: eastern and central North America*. San Diego, CA: Houghton Mifflin Harcourt.
29. Gerhardt HC. 1974 The significance of some spectral features in mating call recognition in the green treefrog (*Hyla cinerea*). *J. Exp. Biol.* **61**, 229–241. (doi:10.1242/jeb.61.1.229)
30. Gerhardt HC. 1987 Evolutionary and neurobiological implications of selective phonotaxis in the green treefrog, *Hyla cinerea*. *Anim. Behav.* **35**, 1479–1489. (doi:10.1016/S0003-3472(87)80020-9)
31. Gerhardt HC, Dyson ML, Tanner SD. 1996 Dynamic properties of the advertisement calls of gray tree frogs: patterns of variability and female choice. *Behav. Ecol.* **7**, 7–18. (doi:10.1093/beheco/7.1.7)
32. Reichert MS, Höbel G. 2015 Modality interactions alter the shape of acoustic mate preference functions in gray treefrogs. *Evolution* **69**, 2384–2398. (doi:10.1111/evo.12750)
33. R Core Team. 2015 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.
34. Sueur J, Aubin T, Simonis C. 2008 Seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics* **18**, 213–226. (doi:10.1080/09524622.2008.9753600)
35. Ligges U, Krey S, Mersmann O, Schnackenberg S. 2018 tuneR: analysis of music and speech. See https://CRAN.R-project.org/package=tuneR.
36. Mendelson TC, Fitzpatrick CL, Hauber ME, Pence CH, Rodríguez RL, Safran RJ, Stern CA, Stevens JR. 2016 Cognitive phenotypes and the evolution of animal decisions. *Trends Ecol. Evol.* **31**, 850–859. (doi:10.1016/j.tree.2016.08.008)
37. Dyson ML, Reichert MS, Halliday TR. 2013 Contests in amphibians. In *Animal contests* (eds ICW Hardy, M Briffa), pp. 228–257. Cambridge, UK: Cambridge University Press.
38. Reichert MS, Gerhardt HC. 2011 The role of body size on the outcome, escalation and duration of contests in the grey treefrog, *Hyla versicolor*. *Anim. Behav.* **82**, 1357–1366. (doi:10.1016/j.anbehav.2011.09.019)
39. Höbel G, Rodríguez RL. 2022 Data from: Positive-to-negative behavioural responses suggest hedonic evaluation in treefrog mate choice. Dryad Digital Repository. (doi:10.5061/dryad.41ns1rndz)