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Original Article

The sound of fear is heritable

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Abstract

The nonlinearity and fear hypothesis predicts that highly aroused vocal mammals and birds produce vocalizations (notably alarm calls and screams) which contain a variety of nonlinear phenomena (NLP). Such vocalizations often sound "noisy" because vocal production systems are over-blown when animals are highly aroused. While much is known about the conditions under which animals produce vocalizations containing NLP and how species respond to them, there is little research about the heritability of such behavioral traits. Using the quantitative genetic animal model, we estimated the genetic basis of "noise" in alarm calls produced by females and found significant heritability in call entropy—our measure of the noisiness. About 9% of the variance in noisiness can be accounted for by genetic differences. Taken together, these findings suggest that the degree to which marmots produce noisy calls is modestly heritable and can be thus subject to further evolution via natural selection.

Key words: acoustic communication, animal model, fear communication, heritability of vocalizations, yellow-bellied marmot.

Vocalizations are the output from a dynamic system and, like other dynamic systems, may have a variety of states. The transition from a steady state creates a set of predictable sounds referred to as nonlinear phenomena (NLP) that may contain important information (Fitch et al. 2002). The nonlinearity and fear hypothesis can be attributed to highly aroused animals overblowing their vocal production system and thus driving these state changes (Blumstein et al. 2008; Blumstein and Récapet 2009). In the acoustic domain, NLP include four classifications: limit cycles (periodic, self-sustained oscillations), subharmonics (energy bands below the fundamental and between the harmonic frequencies), deterministic chaos (irregular vibrations), and bifurcations (transitions between different vibratory behaviors) (Wilden et al. 1998; Fitch et al. 2002). Screams produced in agonistic (Gouzoules et al. 1984) and predatory interactions (Blumstein et al. 2008) are notable in that they contain many NLP. Moreover, as an individual's level of arousal increases, the structure of vocalizations often changes in predictable ways. For instance, when meerkats (*Suricata suricatta*) are exposed to higher-risk predatory situations, their alarm calls become more "noisy" (Townsend and Manser 2011).

Individuals who hear natural sounds containing NLP enhance their response compared to regularly structured calls. Yellow-bellied marmots (*Marmota flaviventer*) decreased the proportion of time allocated to foraging when they heard alarm calls manipulated to contain white noise (used to simulate deterministic chaos (Blumstein and Récapet 2009)). In comparison, calls with added silence did not lead to significantly different responses from controlled and unmanipulated alarm calls. Additionally, meerkats had greater behavioral escape responses to alarm calls containing NLP than those that did not (Townsend and Manser 2011). Another study found that rhesus monkeys (*Macaca mulatta*) who emitted "disorderly" screams subsequently triggered an evocative response in other monkeys (Gouzoules et al. 1984). Thus, alarm calls that contain NLP may elicit specific responses in receivers.

A number of studies have created synthetic NLP and found that they too increase arousal. For instance, great-tailed grackles (*Quiscalus mexicanus*), in reaction to simulated nonlinearities, decreased the time they allocated to relaxed behavior compared to controls (Slaughter et al. 2013). White-crowned sparrows (*Zonotrichia leucophrys*) heightened their behavioral responses to synthesized NLP by increasing their vigilance (Blesdoe and Blumstein 2014). Even non-vocal skink species (*Emoia impar* and *Emoia cyanura*) increased antipredator responses when exposed to white noise, compared to hearing control sounds (Yan et al. 2019; Kelligrew et al. 2021).

Vocalizations with NLP are more difficult to habituate to (Fitch et al. 2002). Species that live in groups are exposed to numerous calls a day, making individuals more likely to ignore calls that do not provide relevant information (e.g., Hare and Atkins 2001; Blumstein et al. 2004). Predictable calls that are easier to habituate to may no longer serve a functional purpose, and, therefore, are ignored to potentially allow for the reception of more meaningful calls. This can be seen when the playback of alarm calls containing NLP (vocalizations emitted in more "urgent" situations were less structured and "noisy" as illustrated by their spectrograms)

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prolonged the latency to relax in meerkats (Townsend and Manser 2011). This delay in relaxation is a finding consistent with a lack of habituation to the calls with NLP (Blumstein et al. 2008; Slaughter et al. 2013). Thus, nonlinearities may represent a behavioral approach to prevent habituation in group settings.

While much is known about the conditions under which NLP are produced (Fitch et al. 2002) and about how animals respond to them (Gouzoules et al. 1984; Blumstein and Récapet 2009; Townsend and Manser 2011), we know relatively little about their genetic basis. Heritability can be measured at the population level and is the proportion of phenotypic variance that can be attributed to a set of unspecified genes (Falconer and Mackay 1998). Traits with significant heritability are those that can potentially respond to natural selection and evolve.

We aimed to estimate whether the "noisiness" (which we define as increased entropy) of yellow-bellied marmot alarm calls was heritable by capitalizing on a 22-year database of alarm call recordings (Blumstein 2007) and a 60-year longitudinal study at the individual level, including a molecular genealogy (Blumstein et al. 2013a). Marmot alarm calls function to communicate predation risk and encode individuality (Blumstein and Armitage 1997; Blumstein and Munos 2005). Individuals are sensitive to variation in caller reliability (Blumstein et al. 2004), and this variation may reflect individual deviation in vulnerability or personality differences. To illustrate this point, socially isolated marmots and marmots with more parasites typically produce noisier calls (Fuong and Blumstein 2019; Nouri and Blumstein 2019), a finding that may reflect the similar vulnerability of those callers. Caller variability may also reflect consistent individual differences in boldness that we have identified in other behavioral traits (Petelle et al. 2013). In the present study, we solely focused on females because they are philopatric, while the majority of males disperse for mating opportunities. Additionally, while all animals emit alarm calls at low rates, females with newly emerged offspring increase their calling (Blumstein et al. 1997), and the propensity to call is associated with increased levels of stress (Blumstein et al. 2006). Prior work has identified significant heritable variation in other marmot alarm call acoustic parameters, but entropy was not quantified in the previous study (Blumstein et al. 2013a). Significant heritable variation in call entropy would suggest a genetic basis of individual variation in an acoustic trait, a phenomenon that has been identified in relatively few species such as zebra finches (*Taeniopygia guttata*, Forstmeier et al. 2009), mice (*Mus musculus*, Thornton et al. 2005) and various insects (e.g., Webb and Roff 1992; Mousseau and Howard 1998; Collins et al. 1999).

Materials and Methods

We studied the heritability of alarm calls in free-living female yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory in Gunnison County, CO, USA. Marmots were regularly live trapped (details in Armitage 2014), and hair was collected from each individual for DNA extraction to create a molecular genealogy (details in Blumstein et al. 2010). We set traps for marmots on mornings and afternoons when it was not excessively hot (> 24 °C) or actively precipitating. Traps were checked within 2 h, and individuals were quickly processed (often ca. 5–10 min, depending on what was required). Because all females were trapped since they emerged from their natal burrows, trapping per se was not particularly stressful. However, on some occasions, marmots emitted alarm calls when we approached the trap. If a marmot alarm called when trapped, we attempted to record these trap-elicited calls using digital recorders (either DAT or solid-state recorders—details in Blumstein and Chi 2012), the structure of which do not differ from more naturally-elicited calls (pers. obs.). While all recordings were digital, we note that the varied recorders may explain some of the variation in call entropy. Nevertheless, trap-elicited vocalizations are high quality recordings because we could standardize the distance to the microphone, attempt to manage environmental noise by angling the microphone away from rivers or other sources of noise, and adjust the microphone's gain. Thus, these calls permitted us to quantify call entropy precisely. Following Fuong and Blumstein (2019), we edited recordings to create up to five files containing a single alarm per calling bout. We selected calls that had limited background noise and created a 0.1 s file that was then normalized using Audacity 2.1.3 (https://www.audacityteam.org/). We quantified entropy, our metric of deterministic chaos, using Sound Analysis Pro (http://soundanalysispro.com/; settings: contrast = 50, segmentation = 50.4 dB, frequency range = 11,025 Hz, FFT data window = 10.0 ms, advance window = 0.23 ms, and contour threshold = 10). We also counted the energy bands (the fundamental plus all harmonics) in the calls, which prior work (Blumstein and Chi 2012) has shown to be positively associated with entropy.

We fitted a model to explain variation in alarm call entropy using a quantitative genetic approach, the animal model (Kruuk 2004). The animal model is a mixed effects model that includes an individual identity as a random effect linked to a pedigree, allowing us to estimate the additive genetic variance of a trait (Kruuk 2004). Given the structure of the data with repeated measures at the individual, bout, year, and colony level, we also included those terms as random effects. Bouts were nested within individuals because some individuals were trapped and called more frequently than others. We included a number of fixed effects to better estimate the additive genetic variation in call entropy. We counted the number of energy bands, which we defined as the fundamental plus harmonics, and included the number of energy bands as a fixed effect because calls with more dynamic range could potentially contain more entropy. We also measured the call's duration and included this as a fixed effect because longer calls could contain more entropy. We included age as a factor (levels: pups, 1-year olds, and adults, individuals ≥ 2 years old), and time of day (AM or PM) because prior work has shown that age influences call structure (Blumstein and Armitage 1997) and prior work has shown that call entropy may vary by time of day (Blumstein and Chi 2012).

The model was fitted using a Bayesian approach with MCMCglmm 2.34 (Hadfield 2010) in R 4.2 (R Core Team 2023). We used a weak prior for random effects with V = 1 and nu = 0.002. We ran 510,000 iterations with a thinning interval of 500 and a burning period of 10,000 iterations. All parameters converged according to the Heidelberger and Welch's convergence diagnostic. Autocorrelation in the posterior was below 0.05 for all parameters. All parameters are reported as the mode of the posterior distribution with their associated 95% highest posterior density intervals (HPDI). Fixed effects were considered different from zero if the HPDI was not overlapping zero. Since variance components are strictly positive, we considered the parameter non-negligible if the lower HPDI was higher than 0.001; a criterion that has been used in similar studies (e.g., Wolak et al. 2018).

Results

After eliminating calls because of poor recording quality, we analyzed 1433 alarm calls from 290 bouts of calls by 140 individuals over 17 years of observations. There were 107, 54, and 129 bouts recorded for pups, yearlings, and adults, respectively. There were 4.9 (± 0.36 SD) calls per bout (range: 2–5). There were 2.1 (± 2.20 SD) bouts per individual (range: 1–14). Of the calls, 81 bouts were recorded in the morning, while 209 were recorded in the afternoon. The average entropy in alarm calls was 0.78 (± 0.44 SD). Alarm calls had an average of 5.5 (± 1.32) energy bands and averaged 37.2 (± 0.96 SD) ms long. The multigenerational pedigree is described in Table 1.

Energy bands, call duration, age, and time of day had a positive effect on call entropy (Table 2). After controlling for these variables, additive genetic, year, and bouts effects were estimated to be different from zero with a conditioned heritability of 0.086 (95% HPDI: 0.001–0.283) (Table 2). Colony and permanent environment effects were negligible and not different from zero (Table 2). Total individual variance (sum of additive genetic, permanent environment, and bouts which were nested within individuals) was 0.224 (0.182–0.300) with a variance ratio of 0.552 (0.429–0.635). Evolvability, the ratio of additive genetic variance, V_a, by the square of the mean, was 0.249 (0.006–0.678).

Table 1. Summary statistics for the pruned pedigree used for animal models of noisiness in alarm calls of yellow-bellied marmots

Variable	Value
Records	260
Maternities	214
Paternities	191
Full sibs	131
Maternal sibs	305
Maternal half sibs	174
Paternal sibs	625
Paternal half sibs	494
Maternal grandmothers	172
Maternal grandfathers	118
Paternal grandmothers	86
Paternal grandfathers	83
Maximum pedigree depth	10
Founders	45
Mean maternal sibship size	2.21
Mean paternal sibship size	3.47
Non-zero F	57
F > 0.125	35
Mean pairwise relatedness	0.043
Pairwise relatedness ≥ 0.125	0.135
Pairwise relatedness ≥ 0.25	0.078
Pairwise relatedness ≥ 0.5	0.024

Discussion

We quantified entropy in alarm calls to quantify call noisiness, which we then used to estimate the magnitude of a specific NLP in marmot alarm calls. By fitting a quantitative genetic animal model, we detected significant genetic variation in the entropy contained in female marmot alarm calls. Given our ability to control for permanent environment, common environment, and the relatively small credible intervals, our inference of genetic variation in alarm call entropy is robust (Kruuk and Hadfield 2007). From this, we conclude that call noisiness has a moderate heritability and evolvability. Given that the nonlinearity and fear hypothesis (Blumstein et al. 2008; Blumstein and Récapet 2009) predicts a relationship between call noisiness and perceived risk, these results suggest that the way in which animals perceive variation in threats has a genetic component.

At some level, this should not be surprising. Personality traits, including those that are associated with risk perception, in many species are repeatable (e.g., Van Oers et al. 2004; Patrick et al. 2013; Mazué et al. 2015), and repeatability provides an upper-limit estimate of heritability (Boake 1989) which suggests that there should be some heritable variation. Prior studies in this population have shown that marmots have significant repeatability of aggression (Blumstein et al. 2013b), exploration and activity (Petelle et al. 2019), and boldness and docility (Petelle et al. 2013). Current research has found significant repeatability and heritability of flight initiation distance (Scurka 2023).

Our heritability estimate of 0.086 for call entropy is relatively small compared to other behavioral traits, which average 0.24 (Dochtermann et al. 2019), and substantially smaller than previous heritability estimates for other acoustic traits which averaged 0.21 (range 0.01–0.48) (Blumstein et al. 2013a). However, since the non-genetic between-individual variance ratio (*pe*^{2}) was 0.004, we note that apart from genetic effects, there is limited among-individual variation. Thus, the low observed heritability for entropy suggests that this trait might have been under strong selection or that alarm calls are strongly context dependent leading to extensive phenotypic variance. This finding is consistent with the nonlinearity and fear hypothesis, which expects NLP only when animals are highly aroused and lose control of their vocal production. However, adult calls were noisier than calls emitted from younger cohorts. In a proximate sense, this finding could reflect a loss of control over their vocal tract. Functionally, however, it also could reflect a greater benefit from warning conspecifics because adults are likely to be surrounded by descendant kin, while pre-reproductive animals are surrounded only by collateral kin.

Significant variation in call entropy was explained by our random effect of year. This could reflect different stresses that vary annually. Environmental factors affect many marmots' life histories and demographic traits (e.g., Armitage 2014; Cordes et al. 2020; Paniw et al. 2020; Conquet et al. 2023). Variation in expected longevity could influence perceptions of risk. Furthermore, predator populations fluctuate over time, and it is possible that variation in exposure to predators explained some variation in how noisy calls were. Identifying the cause(s) of this annual variation requires a more focused study.

Taken together, we have shown that, at the population level, there is significant variation in alarm call noisiness that has a

Table 2. Parameter estimates (posterior mode with 95% HDPI) of alarm call entropy in yellow-bellied marmots

		95% HDP intervals	
	Estimate	Lower	Upper
Fixed effects			
Intercept	−1.806	−2.209	−1.533
Energy Bands	0.035	0.005	0.069
Call Duration	0.022	0.017	0.028
Age: Yearling	0.389	0.228	0.568
Age: Adult	0.474	0.307	0.641
Time of Day	0.112	0.000	0.256
Variance components			
V_{a}	0.049	0.001	0.135
V_{pe}	0.002	0.0002	0.068
V_{bouts}	0.145	0.112	0.201
V_{colony}	0.001	0.0003	0.039
V_{year}	0.053	0.017	0.124
V_{R}	0.134	0.124	0.145
V_{P}	0.419	0.362	0.532
Variance ratio			
h^2	0.086	0.001	0.283
pe^2	0.004	0.0004	0.152
bouts^2	0.362	0.232	0.463
colony^2	0.002	0.001	0.084
year^2	0.117	0.043	0.244

For Age, pups were used as the reference level. V_A, V_{colony}, V_{year}, V_{pe}, and V_{bouts} are the variance components of additive genetic, colony, year, permanent environment, bouts effects with their associated variance ratio h^2 (heritability), pe^2, bouts^2, colony^2, and year^2. V_r is the residual variance and V_P is the phenotypic variance (sum of all variance components). Variance ratios were estimated by dividing the specific variance component by V_P.

genetic basis. While the heritability estimate is modest, there is significant evolvability in call noisiness. Heritability in the entropy of alarm calls creates the potential for noisier alarm calls to be favored, perhaps because calls with NLP relay more information. This means that, given sufficient selection, there is an opportunity to evolve to a new average noisiness, which may result from individuals becoming habituated to more noisy calls. Our study has demonstrated that the sound of fear is heritable. Future studies expanding on these findings can focus on identifying the situations that are selected for modulating noisiness and other NLP in alarm calls.

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Authors' Contributions

D.T.B.: conceptualization, data collection, results interpretation, writing—original draft, supervision, funding, review, and editing; N.V.: data management, results interpretation, writing—original draft, review, and editing; M.E.: data collection, data analysis, results interpretation, review, and editing; L.V.: data management, review, and editing; J.G.A.M.: data collection, data management, data analysis, results interpretation, writing—original draft, review and editing. All authors approved the final submission.

Conflict of Interest statement

The authors declare that they have no competing interests.

Ethics Statement

Data were collected under the UCLA Institutional Animal Care and Use protocol (2001-191-01, renewed annually) and with permission from Colorado Parks and Wildlife (TR917, renewed annually).

Data Availability

Data and code are archived at OSF: https://osf.io/d8prg/.

References

Armitage KB, 2014. *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*. Cambridge: Cambridge University Press.

Blesdoe EK, Blumstein DT, 2014. What is the sound of fear? Behavioral responses of white-crowned sparrows *Zonotrichia leucophrys* to synthesized nonlinear acoustic phenomena. *Curr Zool* **60**:534–541.

Blumstein DT, 2007. The evolution, function, and meaning of marmot alarm communication. *Adv Study Behav* **37**:371–401.

Blumstein DT, Armitage KB, 1997. Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Anim Behav* **53**:143–171.

Blumstein DT, Chi YY, 2012. Scared and less noisy: Glucocorticoids are associated with alarm call entropy. *Biol Lett* **8**:189–192.

Blumstein DT, Lea AJ, Olson LE, Martin JGA, 2010. Heritability of anti-predatory traits: vigilance and locomotor performance in marmots. *J Evol Biol* **23**:879–887.

Blumstein DT, Munos O, 2005. Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. *Anim Behav* **69**:353–361.

Blumstein DT, Nguyen KT, Martin JGA, 2013a. Ontogenetic variation of heritability and maternal effects in yellow-bellied marmot alarm calls. *Proc Biol Sci* **280**:20130176.

Blumstein DT, Patton ML, Saltzman W, 2006. Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biol Lett* **2**:29–32.

Blumstein DT, Petelle MB, Wey TW, 2013b. Defensive and social aggression: Repeatable but independent. *Behav Ecol* **24**:457–461.

Blumstein DT, Récapet C, 2009. The sound of arousal: The addition of novel non-linearities increases responsiveness in marmot alarm calls. *Ethology* **115**:1074–1081.

Blumstein DT, Richardson DT, Cooley L, Winternitz J, Daniel JC, 2008. The structure, meaning and function of yellow-bellied marmot pup screams. *Anim Behav* **76**:1055–1064.

Blumstein DT, Steinmetz J, Armitage KB, Daniel JC, 1997. Alarm calling in yellow-bellied marmots: II. The importance of direct fitness. *Anim Behav* **53**:173–184.

Blumstein DT, Verenyre L, Daniel JC, 2004. Reliability and the adaptive utility of discrimination among alarm callers. *Proc Roy Soc B* **271**:1851–1857.

Boake CRB, 1989. Repeatability: its role in evolutionary studies of mating behavior. *Evol Ecol* **3**:173–182.

Collins RD, Jang Y, Reinhold K, Greenfield MD, 1999. Quantitative genetics of ultrasonic advertisement signalling in the lesser waxmoth *Achroia grisella* (Lepidoptera: Pyralidae). *Heredity* **83**(Pt 6):644–651.

Conquet E, Ozgul A, Blumstein DT, Armitage KB, Oli MK et al., 2023. Demographic consequences of changes in environmental periodicity. *Ecology* **104**:e3894.

Cordes LS, Blumstein DT, Armitage KB, Caradonna PJ, Childs DZ et al., 2020. Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proc Natl Acad Sci USA* **117**:18119–18126.

Dochtermann NA, Schwab T, Anderson Berdal M, Dalos J, Royauté R, 2019. The heritability of behavior: A meta-analysis. *J Hered* **110**:403–410.

Falconer DS, Mackay TF, 1998. *Introduction to Quantitative Genetics*. 4th edn. Essex: Longman.

Fitch WT, Neubauer J, Herzel H, 2002. Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Anim Behav* **63**:407–418.

Forstmeier W, Burger C, Temnow K, Derégnaucourt S, 2009. The genetic basis of zebra finch vocalizations. *Evolution* **63**:2114–2130.

Fuong H, Blumstein DT, 2019. Social security: less socially connected marmots produce noisier alarm calls. *Anim Behav* **154**:131–136.

Gouzoules S, Gouzoules H, Marler P, 1984. Rhesus monkey (*Macaca mulatta*) screams: representational signalling in the recruitment of agonistic aid. *Anim Behav* **32**:182–193.

Hadfield JD, 2010. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R Package. *J Stat Soft* **33**:1–22.

Hare JF, Atkins BA, 2001. The squirrel that cried wolf: reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). *Behav Ecol Sociobiol* **51**:108–112.

Kelligrew C, Tian S, Weiss M, Williams DM, Blumstein DT, 2021. The effect of white noise on behavioral and flight responses of blue-tailed skinks. *Curr Zool* **67**:125–126.

Kruuk LEB, 2004. Estimating genetic parameters in natural populations using the 'animal model'. *Philos Trans R Soc London Ser B* **359**:873–890.

Kruuk LEB, Hadfield JD, 2007. How to separate genetic and environmental causes of similarity between relatives. *J Evol Biol* **20**:1890–1903.

Mazué GPF, Dechaume-Moncharmont FX, Godin JGJ, 2015. Boldness-exploration behavioral syndrome: Interfamily variability and repeatability of personality traits in the young of the convict cichlid (*Amatitlania siquia*). *Behav Ecol* **26**:900–908.

Mousseau TA, Howard DJ, 1998. Genetic variation in cricket calling song across a hybrid zone between two sibling species. *Evolution* **52**:1104–1110.

Nouri K, Blumstein DT, 2019. Parasites are associated with noisy alarm calls. *Front Ecol Evol* **7**:28.

Paniw M, Childs DZ, Armitage KB, Blumstein DT, Martin JGA et al., 2020. Assessing seasonal demographic covariation to understand environmental-change impacts on a hibernating mammal. *Ecol Lett* **23**:588–597.

Patrick SC, Charmantier A, Weimerskirch H, 2013. Differences in boldness are repeatable and heritable in a long-lived marine predator. *Ecol Evol* **3**:4291–4299.

Petelle MB, Martin JGA, Blumstein DT, 2019. Mixed support for state maintaining risky personality traits in yellow-bellied marmots. *Anim Behav* **150**:177–188.

Petelle MB, McCoy DE, Alejandro V, Martin JGA, Blumstein DT, 2013. Development of boldness and docility in yellow-bellied marmots. *Anim Behav* **86**:1147–1154.

R Core Team, 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Scurka MA, 2023. *The Heritability of Fear: Decomposing Sources of Variation in Marmot Flight Initiation Distance. Master of Science Thesis*, Department of Ecology and Evolutionary Biology, University of California Los Angeles.

Slaughter EI, Berlin ER, Bower JT, Blumstein DT, 2013. A test of the nonlinearity hypothesis in the great-tailed grackle (*Quiscalus mexicanus*). *Ethology* **119**:309–315.

Thornton LM, Hahn ME, Schanz N, 2005. Genetic and developmental influences on infant mouse ultrasonic calling. III. Patterns of inheritance in the calls of mice 3-9 days of age. *Behav Genet* **35**:73–83.

Townsend SW, Manser MB, 2011. The function of nonlinear phenomena in meerkat alarm calls. *Biol Lett* **7**:47–49.

Van Oers K, Drent PJ, De Goede P, Van Noordwijk AJ, 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proc Biol Sci* **271**:65–73.

Webb KL, Roff DA, 1992. The quantitative genetics of sound production in *Gryllus firmus*. *Anim Behav* **44**:823–832.

Wilden I, Tembrock G, Herzel H, Peters G, 1998. Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics* **9**:171–196.

Wolak ME, Arcese P, Keller LF, Nietlisbach P, Reid JM, 2018. Sex-specific additive genetic variances and correlations for fitness in a song sparrow (*Melospiza melodia*) population subject to natural immigration and inbreeding. *Evolution* **72**:2057–2075.

Yan KM, Pinto SP, Vartany C, Blumstein DT, 2019. Shift down, look up: A test of the non-linearity and fear hypothesis in a non-vocal skink. *Ethology* **125**:153–158.