



Is the propensity to alarm-call heritable and related across multiple contexts?

Daniel T. Blumstein ^{a, b, *}, Caleb J. Velasquez ^a, Katie A. Adler ^{a, b}, Julien G. A. Martin ^{b, c}

^a Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, U.S.A.

^b The Rocky Mountain Biological Laboratory, Crested Butte, CO, U.S.A.

^c Department of Biology, University of Ottawa, Ottawa, ON, Canada

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Alarm calling is an important antipredator behaviour by which individuals alert conspecifics and heterospecifics of possible danger and/or ward off potential predators. The propensity to utter calls may reflect the amount of risk an individual experiences and a variety of other internal and environmental factors that may be context and species specific. However, whether the propensity to utter alarm calls is heritable has not been studied. Using a quantitative genetic animal model, we estimated the heritability of alarm calling in yellow-bellied marmots, *Marmota flaviventris*. We found significant heritability in the propensity to utter naturally elicited alarm calls (0.06) and trap-elicited alarm calls when marmots were trapped (0.21). There was a small but significant genetic correlation between these traits (0.338). Together, these results show that the propensity to utter alarm calls is individually variable and context dependent and can evolve in response to natural selection.

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Alarm calling is a common antipredator behaviour (Blumstein, 2007; Caro, 2005; Kavaliers & Choleris, 2001; Klump & Shalter, 1984), but not all individuals utter calls when they detect a predator (reviewed in Butler et al., 2017; Hollén & Radford, 2009). Alarm calling presents a paradox in that calls may function to warn conspecifics or heterospecifics about the presence of predators (Evans et al., 1993; Krams et al., 2006; R. Smith, 1986), but by doing so calling attracts a predator's attention (Haff & Magrath, 2011; Magrath et al., 2015). Some studies have addressed the paradox by noting that callers may only utter calls when they are in relatively safe locations (Collier et al., 2010; Sherman, 1985; Townsend et al., 2012), and calls may also function to actively deter predators (Perrins, 1968; Zuberbühler, 1999), so they may not be that costly after all. There are many studies that have shown that the structure of calls varies as a function of predation risk (Manser, 2001; Price et al., 2015). Thus, while many internal and external factors may explain variation in call structure (e.g. parasite status: Nouri & Blumstein, 2019; physiological stress: Blumstein & Chi, 2012), some studies have shown that alarm call structure is individually distinctive (Blumstein & Munos, 2005; Dhondt & Lambrechts, 1992; Loughry et al., 2019; Warrington et al., 2015) and is to

some extent heritable (Blumstein et al., 2013; Blumstein, Vu, et al., 2024). Prior work has also shown that the propensity to utter calls also varies as a function of risk (Blumstein & Armitage, 1997; Wheeler, 2008) and that individuals vary in their propensity to call (Nash et al., 2020; Schwarting, 2023). Remarkably, there are no studies that have studied the heritability of the propensity to call.

Like alarm calling, individuals may consistently vary in how they express their antipredator behaviour and, in a variety of species, some antipredator behaviours are repeatable, which means there are consistent differences among individuals (Bell et al., 2009). Reduced activity, the likelihood to run away, how long an individual stays in refuge and the behaviour while fleeing are all repeatable to some extent. Ehlman et al. (2019) observed repeatable differences in activity levels (less movement while swimming) of mosquitofish, *Gambusia affinis*, following exposure to predator cues. Krams et al. (2014) found high repeatability in yellow mealworm beetles, *Tenebrio molitor*, tonic immobility, a coma-like behaviour where animals freeze up when threatened (Marx et al., 2008). In field crickets, *Gryllus integer*, individuals differed in how long they spent hiding based on relative predation risk of their home environment, a repeatable trait when studied in the laboratory (Hedrick & Kortet, 2006). Brodie and Russell (1999) found that there was little variation and high repeatability in individual garter snakes' (*Thamnophis ordinoides*) fleeing behaviour.

* Corresponding author.

E-mail address: marmots@ucla.edu (D. T. Blumstein).

Repeatability provides an upper limit on heritability because a trait cannot have a heritability estimate that exceeds its repeatability (Boake, 1989; Chervet et al., 2011; Falconer, 1981). However, it is important not to assume a phenotypic gambit and to estimate heritability because it helps us understand the genetic basis of complex traits. Some antipredator behaviours, like temperament towards predators (e.g. boldness or fearfulness) and vigilance, have significant heritability estimates. The decision to stay and defend their young instead of flushing from their nests in alpine swifts, *Tachymarpis melba*, is heritable within certain colonies (Bize et al., 2011). In yellow-bellied marmots, *Marmota flaviventer*, antipredator vigilance had low, but significant, heritability (Blumstein et al., 2010). Two different source populations (riparian versus grasslands) of funnel-web spiders (*Agelenopsis aperta*) had different heritability estimates of their antipredator behaviour as a function of their source environment (Riechert & Hedrick, 1990).

Yellow-bellied marmots are an ideal system in which to study the heritability of the propensity to utter alarm calls and to better understand the quantitative genetics of antipredator behaviours. These marmots have been studied for over six decades at the Rocky Mountain Biological Laboratory (RMBL), located in Gothic, Colorado, U.S.A. (Armitage, 2014; Blumstein, 2013). Naturally occurring and trap-elicited bouts of marmot alarm calling have been recorded for over 20 years, during which time we also created a molecular genealogy. This provides a rare opportunity to study individual alarm calling behaviours across multiple generations in the wild, which is important because heritability estimates are environment specific (Furrow et al., 2011; Hoffmann et al., 2016; Wilson et al., 2006) and it is important to estimate it in the wild. During this longitudinal study, many different aspects of alarm calling have been examined.

At the population level, marmots alarm-call at variable rates; some individuals are never observed to call (Blumstein & Armitage, 1997). Marmot docility, a personality trait that includes in its calculation the propensity to utter alarm calls when trapped, is repeatable and heritable (Martin et al., 2017; Petelle et al., 2013). Subsequent work using social network analyses showed that less ‘popular’ marmots have a greater propensity to alarm call (Fuong et al., 2015). Health status also influences the propensity to utter alarm calls; marmots infected with trypanosomes produced alarm calls at marginally higher rates than uninfected individuals or than those with a different infection, while individuals infected with *Ascaris* were less likely to call when trapped (Nash et al., 2020). What remains to be properly studied is whether significant variation in the propensity to utter alarm calls is heritable. The aim of this study was to estimate the heritability to utter calls in two different contexts (naturally, and when individuals were trapped) and the genetic correlation between these two measures.

METHODS

From 2002 to 2022, yellow-bellied marmots were both regularly trapped and extensively observed (ca. 1000 h/year) in and around the Rocky Mountain Biological Laboratory (RMBL; 38°57’N, 106°59’W), located in Gunnison County, Colorado, U.S.A. We used established techniques to live-trap and mark individuals for observation from afar (Armitage, 1982). Briefly, trapped individuals were marked with unique eartags and unique symbols painted on their back with nontoxic fur dye to facilitate identification. For each trapping event, we recorded whether an individual called when we approached the trap.

Marmot colonies were observed during peak hours of activity, between 0700 and 1100 hours and between 1630 and 1900 hours

(Armitage, 1962). Trained observers used spotting scopes and binoculars at distances of 20–150 m from individuals to avoid disrupting their natural behaviours (Blumstein, 2013). During observation periods, we noted all instances of alarm calling and, when possible, the stimulus that elicited the call and the caller’s identity.

We focused on bouts of calling (a bout of calling contained 1–3611 alarm calls). We characterized alarm calling in two different conditions: naturally elicited calls from identified individuals and trap-elicited alarm calls. For observed bouts of natural calling, the rate of alarm calling was calculated as the total number of calling bouts produced by an individual in a given year divided by the total time its colony (a geographical location where marmots live) was observed on days when individuals were observed. Alarm calling for trapped individuals was the proportion of trapping events in a given year in which an individual produced alarm calls. While we had not previously estimated the repeatability of calling, we calculated these annual rates because a number of both internal and contextual factors that could influence the propensity to call vary annually. Marmot age was categorized as juvenile (i.e. young of the year), yearling or adult (those in their second year of life or older). We determined predator exposure by calculating a predator index. During our observation sessions we recorded all predator sightings (they were relatively rare). For each colony and in each year, we calculated the proportion of observation sessions where one or more predators were detected. Using a median split, we classified those above the median as having a high predation index and those below the median as having a low predation index. Colony size (range 1–49; mean $\pm$ SD = 12.23 $\pm$ 11.31) was defined as the total number of yearlings and adults seen and/or trapped. For a few individuals who may have been seen/trapped at multiple sites, we included them in the colony size of the site where they were seen/trapped the most.

Once a year, we collected hair samples of trapped individuals from which we extracted DNA and quantified genetic variation in 12 microsatellite loci (Blumstein et al., 2010). Based on field observations and these genetic data, we identified sires and dams for each individual (Blumstein et al., 2009; Goossens et al., 1998) and used these to create a multigenerational genealogy. Our genealogy spanned 11 generations and contained 2196 individuals (Table 1).

Table 1
Summary statistics of the pedigree used in the analysis of alarm call propensity in yellow bellied-marmots

Variables	Value
Records	2196
Maternities	1950
Paternities	1849
Full sibs	8336
Maternal sibs	17 393
Maternal half sibs	9057
Paternal sibs	44 664
Paternal half sibs	36 328
Maternal grandmothers	1678
Maternal grandfathers	1352
Paternal grandmothers	860
Paternal grandfathers	820
Maximum pedigree depth	11
Founders	175
Mean maternal sibship size	10
Mean paternal sibship size	17.28
Nonzero <i>F</i>	598
<i>F</i> > 0.125	348
Mean pairwise relatedness	0.037
Pairwise relatedness $\geq$ 0.125	0.12
Pairwise relatedness $\geq$ 0.25	0.06
Pairwise relatedness $\geq$ 0.5	0.013

Fitting the Animal Model

The quantitative genetic animal model is a method of variance decomposition that permits us to estimate heritability in the wild (Wilson et al., 2010). The animal model is a type of mixed-effects model that decomposes phenotypic variation into genetic and nongenetic variance using among-individual relatedness (derived from a pedigree) (Wilson et al., 2010). We fitted a bivariate animal model of alarm calling with both the rate of alarm calling during observations (log-transformed) and the probability of calling when trapped as response variables. Alarm calling during observations was log-transformed and fitted with a Gaussian distribution error and, thus, the heritability values were estimated on the observed scale. The probability to call when trapped (number of times an individual called when in a trap versus total number of times trapped within a given year) was fitted with a binomial error distribution with a probit link function. Because this was a non-Gaussian trait, heritability values were estimated on the latent scale (probit transformed) and had to be backtransformed so that we could interpret them on the observed scale. We report values both in the latent and observed scale. Age, sex, valley position (we have a set of higher- and lower-elevation sites and coded these down valley or up valley), colony size (the number of adult marmots living at a colony site that year) and predation index were included as fixed effects for both traits. We calculated the predator index for each colony, and for each year, as the proportion of observation periods where at least one predator was detected (details in Blumstein et al., 2023). We used a median split to assign colony years with rates of predator detection below the median as 'low predation pressure' and those with rates above the median as 'high predation pressure'. We used random effects to estimate additive genetic, permanent environment, year of observation and colony variance for both alarm-calling traits and their correlation at the level of each random effect (i.e. genetic, permanent environment, year and colony correlation between calling traits). Note that the among-individual variance used to estimate repeatability equals the sum of the genetic and permanent environment variance.

The model was fitted using 'MCMCglmm' function from the 'MCMCglmm' package (Hadfield, 2010) in R version 4.4.0 (R Core Team, 2024). We used weakly informative prior for the random effects following de Villemeurieuil (2023; $V = \text{diag}(2)$, $\nu = 2$, $\alpha.\mu = c(0, 0)$, $\alpha.V = \text{diag}(2)$). We ran the model for 610 000 iterations, with a burn-in of 10 000 and a thinning interval of 600 to obtain posterior distribution with 1000 independent iterations. The autocorrelation for all parameters was below 0.1 and all parameters passed the Heidelberger and Welch diagnostic test of convergence.

Ethical Note

Marmots were studied under annual permits issued by the Colorado Division of Wildlife (TR-917). All procedures were approved under research protocol ARC 2001-191-01 by the University of California, Los Angeles Animal Care Committee on 13 May 2002 and renewed annually. As outlined in Blumstein et al. (2023), individuals were live-trapped and marked to facilitate observations. Traps were set in the morning and late afternoon (only when it was cool) and checked within 2 h of setting. Trapped marmots were processed quickly (within 5–15 min depending upon what needed to be done) and released at the point of capture. Prior work has shown that only those individuals that struggle in the trap (relatively few of them) have an increased glucocorticoid response (Smith et al., 2012). The majority of trapping events were with relaxed individuals. These trapping methods have been used for 62 years at the study site and there is no detectable effect on population viability.

RESULTS

We recorded 4101 observations made up of both naturally observed marmots and trapped individuals. We found that both traits were repeatable and heritable (Table 2). The heritability (h^2) of alarm calls observed in the natural environment was 0.05 and the heritability of trap-elicited calls was 0.21 on the latent (probit transformed) scale and 0.11 (0.07, 0.15) on the observed scale. The genetic correlation between naturally and trap-elicited alarm calling was 0.338. The low genetic correlation suggests that these traits are similar but are not identical at the genetic level.

We detected significant random effects of an individuals' permanent environment, year and colony (Table 2). In addition, there were significant age, sex, predation index and colony size effects (Table 2, Supplementary Figs. S1–S5). There was a negative effect of colony size on observation rates, where there was less calling in larger groups, but this had no effect on trap-elicited rates. Juveniles alarm-called more often in both contexts than adults, and males called more in traps than females (Table 2).

DISCUSSION

We have shown for the first time that the propensity to utter alarm calls is heritable but that the trait is dependent on context. The low, but significant, heritability estimates highlight the importance of other internal and external factors in explaining the propensity to utter alarm calls.

While the propensity to utter calls is heritable, the genetic correlation between the two contexts (during observations and in traps) was significant but low, which suggests that these traits are

Table 2

Parameters estimated from a bivariate animal model of alarm-calling rate during observation and propensity to call when trapped in yellow-bellied marmots

Parameters	Rate of call during observations (median [95% HDPI])	Probability to call when trapped (median [95% HDPI])
Fixed effects		
Intercept	0.462 [-0.040, 1.105]	-2.026 [-2.776, -1.371]
Predation index (high)	-0.020 [-0.174, 0.144]	0.211 [-0.053, 0.413]
Valley (up)	0.161 [-0.655, 0.724]	-0.894 [-1.594, -0.073]
Colony size	-0.015 [-0.023, -0.008]	-0.011 [-0.023, 0.002]
Sex (male)	0.025 [-0.112, 0.153]	0.173 [0.015, 0.394]
Age (juveniles)	0.284 [0.079, 0.472]	0.745 [0.538, 0.976]
Age (yearlings)	-0.237 [-0.372, -0.095]	0.134 [-0.104, 0.361]
Random effects		
Additive genetic	0.076 [0.013, 0.148]	1.302 [0.969, 1.798]
Permanent environment	0.008 [<0.001, 0.054]	0.316 [0.041, 0.565]
Year	0.143 [0.052, 0.318]	0.135 [0.048, 0.281]
Colony	0.241 [0.039, 0.736]	0.143 [<0.001, 0.690]
h^2	0.051 [0.003, 0.118]	0.206 [0.149, 0.270]
pe^2	0.010 [<0.001, 0.054]	0.052 [0.008, 0.095]
$year^2$	0.101 [0.028, 0.201]	0.020 [0.008, 0.043]
$colony^2$	0.232 [0.048, 0.468]	0.027 [<0.001, 0.173]
r^2	0.066 [0.016, 0.135]	0.259 [0.211, 0.306]
Covariance/Correlations		
Additive genetic	0.107 [-0.002, 0.215] / 0.353 [0.004, 0.682]	
Permanent environment	-0.007 [-0.090, 0.031] / -0.245 [-0.987, 0.586]	
Year	-0.024 [-0.141, 0.064] / -0.193 [-0.691, 0.390]	
Colony	-0.050 [-0.343, 0.174] / -0.393 [-0.951, 0.425]	

Estimates are reported as the posterior median with the 95% highest posterior density interval (HPDI). Fixed effects, covariances and correlations for which the HPDI did not overlap 0 are in bold. Variance components and ratios in bold have a lower HPDI ≥ 0.001 . Variance and ratios for the probability to call when trapped are reported on the latent scale. Variance ratios (h^2 : additive genetic; pe^2 : permanent environment; $year^2$: year; $colony^2$: colony) were estimated as the ratio of a given variance component divided by the sum of all variance components including the residual variance. Repeatability, r^2 , was estimated as the sum of additive genetic and permanent environment variance divided by the sum of all variance components.

not identical. Our heritability estimates were higher for trap-elicited calls ($h^2 = 0.21$ on the latent scale and 0.10 on the observed scale) than for naturally observed calls ($h^2 = 0.06$). In addition, we detected a significant year and colony random effect for naturally elicited calls but not for calls when trapped. The year effect might be associated with annual variation in predator presence not captured by our predation index but also due to interannual variation in observation effort. Given that colony had an effect only for naturally elicited calls but not for calls in the trap suggests that the large variance associated with colony in the naturally elicited alarm calls encompasses a variety of microenvironmental effects directly related to predation risk, such as variation in the availability of cover or visibility. While it is often reported that heritability estimates in the wild are lower than in captivity (e.g. Stirling et al., 2002), heritability estimates do not always differ when measured in controlled (captive) situations and in the wild (Dochtermann et al., 2019).

Our heritability estimates fell within the range of heritability estimates of other antipredator traits in a large range of species. For instance, alpine swifts' propensity to flush had a heritability estimate of 0.146 (Bize et al., 2011). Rhesus macaque, *Macaca mulatta*, antipredator vigilance had a heritability estimate of 0.02–0.23 (Bethell et al., 2019). Sinn et al. (2006) measured the heritability of a variety of dumpling squid (*Euprymna tasmanica*) antipredator behaviours, which ranged from 0.2 to 0.8. Garter snake antipredator displays had an $h^2 = 0.37$ for individual trials and an $h^2 = 0.45$ as an average (Arnold & Bennett, 1984). Aggressiveness in blue tits, *Cyanistes caeruleus*, had a heritability estimate of 0.35 (Class et al., 2014). Overall, this suggests that the heritability of natural and trap-elicited calls as calculated in this study are consistent with other studies on the heritability of antipredator behaviour.

This is important because it shows that quantitative genetic variation for a variety of antipredator behaviours is maintained in natural populations. Thus, antipredator behaviour could further evolve if subjected to directional selection on these traits. It also raises a question of what maintains this quantitative variation. Future studies are required to tease apart age- and sex-related selection on antipredator behaviour traits and to better understand whether fluctuating environmental drivers maintain genetic variation in these traits.

The difference in the heritability estimates from those calculated from natural observations and those calculated from the propensity to call when trapped may reflect how the data were collected. While we could determine with certainty whether an animal called when trapped, we could neither always identify the caller in natural bouts nor hear all naturally elicited alarm calls. This was both because in the wild marmots typically produced one or few alarm calls in a bout, which meant that we were not certain which animal called, and because we could not always identify the animal based on its fur mark. Overall, this led to an underestimation of the rate of alarm calling in nature for some individuals and also increased the phenotypic variance of the trait. There was also more variation in the circumstances associated with naturally elicited calls compared to trap-elicited calls.

Interestingly, we found an effect of colony size on naturally elicited calls but not on the propensity to call when trapped. Alarm-calling rate per individual decreased, on average, when colony size increased, suggesting that our measure of alarm calling during observations, despite its limitations, captures predation risk-related alarm calls. We also found that juveniles called more frequently than adults in both contexts (naturally and when trapped). It is unclear why juvenile and adult rates of calling would differ. One reason might be that juveniles face greater risks because of their small size or because they must learn what is threatening (see also Cheney & Seyfarth, 1990). Alternatively, it might be due to selective

disappearance of individuals calling more frequently as juveniles and thus attracting predators (Blumstein, Adler, & Uy, 2024). Future work investigating the ontogeny of alarm calling from juvenile to adulthood and the age-specific selection on calling is warranted.

The relatively small genetic correlation between alarm calling in the two different contexts (natural and trap-elicited calling) suggests that there may not be many shared loci that explain alarm calling in these different contexts (Gardner & Latta, 2007). More importantly, this is a strong indication that the propensity to alarm-call when trapped differs from that of naturally observed alarm calling. Thus, studies focusing only on one of the two contexts should be careful in their general ecological interpretation of the measured trait. These results suggest that an individual's propensity to call when trapped is an imperfect indicator of the natural propensity to utter alarm calls (contra Blumstein et al., 1997) despite the fact that the acoustic structure of the calls produced in the two contexts are acoustically similar (D. T. Blumstein, personal observation).

Future work that obtains better estimates of caller identity (perhaps through the use of wearable or embedded microphones) would be essential to determine whether the low genetic correlation reflects measurement error or whether there are biologically important differences in the context of natural versus trap-elicited calling. Indeed, one difference is that when animals call in traps, we, to some extent, have controlled for a variety of environmental factors, including the predator type, and should expect greater heritability estimates. Regardless, and importantly, these results show that the propensity to utter alarm calls is individually variable and can evolve in response to natural selection.

Data Availability

Data and code to reproduce these analyses are available at OSF: <https://osf.io/vcuhn/>.

Author Contributions

Daniel T. Blumstein: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Caleb J. Velasquez:** Writing – review & editing, Writing – original draft, Investigation. **Katie A. Adler:** Writing – review & editing, Formal analysis, Data curation. **Julien G.A. Martin:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Interest

None.

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Supplementary Material

Supplementary Material associated with this article is available, at <https://doi.org/10.1016/j.anbehav.2025.123103>.

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