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Proc. R. Soc. B 2013 **280**, 20130176, published 6 March 2013

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Cite this article: Blumstein DT, Nguyen KT, Martin JGA. 2013 Ontogenetic variation of heritability and maternal effects in yellow-bellied marmot alarm calls. *Proc R Soc B* 280: 20130176.
<http://dx.doi.org/10.1098/rspb.2013.0176>

Received: 24 January 2013

Accepted: 12 February 2013

Subject Areas:

behaviour, evolution, genetics

Keywords:

heritability, mammalian vocalizations, alarm calls, yellow-bellied marmots

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2013.0176> or via <http://rsob.royalsocietypublishing.org>.

Ontogenetic variation of heritability and maternal effects in yellow-bellied marmot alarm calls

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Individuals of many species produce distinctive vocalizations that may relay potential information about the signaller. The alarm calls of some species have been reported to be individually specific, and this distinctiveness may allow individuals to access the reliability or kinship of callers. While not much is known generally about the heritability of mammalian vocalizations, if alarm calls were individually distinctive to permit kinship assessment, then call structure should be heritable. Here, we show conclusively for the first time that alarm call structure is heritable. We studied yellow-bellied marmots (*Marmota flaviventris*) and made nine quantitative measurements of their alarm calls. With a known genealogy, we used the animal model (a statistical technique) to estimate alarm call heritability. In juveniles, only one of the measured variables had heritability significantly different from zero; however, most variables had significant maternal environmental effects. By contrast, yearlings and adults had no significant maternal environmental effects, but the heritability of nearly all measured variables was significantly different from zero. Some, but not all of these heritable effects were significantly different across age classes. The presence of significantly non-zero maternal environmental effects in juveniles could reflect the impact of maternal environmental stresses on call structure. Regardless of this mechanism, maternal environmental effects could permit kinship recognition in juveniles. In older animals, the substantial genetic basis of alarm call structure suggests that calls could be used to assess kinship and, paradoxically, might also suggest a role of learning in call structure.

1. Introduction

Animal vocalizations contain a plethora of potential information that may include information about the signaller's size [1,2], arousal level [3–6], identity [7–9], age [8,10,11] and sex [12]. Indeed, mammalian alarm calls have been shown to be individually distinctive, and this distinctiveness permits receivers to obtain information about the reliability or potential kinship of callers (yellow-bellied marmots, *Marmota flaviventris* [13]; great gerbil, *Rhombomys opimus* [14]; Belding's ground squirrels, *Spermophilus beldingi* [15]; putty-nosed monkeys, *Cercopithecus nictitans* [16]; baboons, *Papio cynocephalus ursinus* [17]; Thomas langurs, *Presbytis thomasi* [18]; cotton-top tamarins, *Saguinus oedipus* [19]; meerkats, *Suricata suricatta* [20]). While such individuality may not necessarily be used by receivers [20,21], in many cases it is. Most of the hypotheses about the value of individually distinctive alarm calls centre on the role they may play in reliability assessment [22], and none have tested the key assumption about kinship, despite many studies that show that alarm calling may be a kin-selected trait [23].

Distinctiveness for individual recognition [24,25] and group or family identity vocal signatures [26] could be obtained by social learning, a mechanism that does not require a genetic basis of vocalization structure. Three orders of birds have the ability to learn vocalizations [27], but learning vocalizations is much less common in mammals [28,29]. However, bats [30,31], pinnipeds [32],

cetaceans [33,34], elephants [35] and ungulates [36] are capable of some degree of vocal learning, which may include the production of group identity signatures [26] and increasing individual discriminability [24,25].

However, if individuals benefit from producing individually distinctive alarm calls, we might expect heritable individual differences in call structure [37]. More generally, we might expect that when individuals benefit from discriminating between kin and non-kin, heritable variation in vocalizations should be selected [38,39]. In species where social groups are formed of relatives, heritable signals can effectively indicate group affiliation and may be used to determine the level of relatedness between individuals [37]. Such heritable traits should be relatively canalized.

Remarkably, given the relatively canalized nature of mammalian vocalizations, relatively little is known about their heritability. A genetic basis of vocalizations has been shown in several mammals (evening bats, *Nycticeius humeralis* [39]; noctule bats, *Nyctalus noctula* [40]; gibbons, *Hylobates* spp. [41,42]; wolves, *Canis lupus*, and dogs, *Canis familiaris* [43,44]; Belding's ground squirrels [15]). However, the heritability of alarm calls was never formally estimated and other potential sources of variation were not identified.

Using the animal model, a quantitative technique that permits the decomposition of variance components [45,46], we estimated the heritability, maternal and permanent environment effects of a set of acoustic features in individually distinctive yellow-bellied marmot alarm calls [13]. Previous work has demonstrated that marmots are capable of discriminating among individuals based on their calls alone [11], and that assessing perceived caller reliability is likely to be the key factor that has selected for the evolution of discrimination abilities [47]. However, if discriminating among kin is an important function of individually distinctive calls, we would expect these individually distinctive factors to be heritable [38,39]. Also, the value of identifying kin might vary over time and be based on caller age. Thus, we analysed heritability separately for juvenile marmots and older animals to gain insights into how the importance of heritability and the maternal environment varied over time.

2. Material and methods

We studied free-living marmots in the East River Valley in and around the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, CO, USA (38°57'29" N, 106°59'06" W; elevation approx. 2890 m) [48]. Marmots at this site have been studied continuously for the past 51 years [48] and their alarm vocalizations have been studied for over a decade [13,23]. Marmots are facultatively social and mothers may recruit daughters to form matrilineal groups [48]. Thus, many animals find themselves in multi-age groups comprising relatives. Social groups and social group membership are known [49]. Detailed methods of marmot trapping and marking can be found in a paper by Armitage [50].

We measured 3250 alarm calls (1706 juvenile alarm calls and 1544 calls from yearlings and adults) from 235 juveniles and 118 yearlings and adults recorded during 650 calling events when marmots were trapped between 2002 and 2010. Individuals were from 203 litters born from 78 mothers. Detailed methods of the recording, editing and normalization of calls can be found elsewhere [13], but the goal was to record five alarm calls from each bout of calls emitted when a marmot called when it was trapped. We calculated spectrograms and the average spectrum using the bioacoustics program CANARY (spectrogram: fast

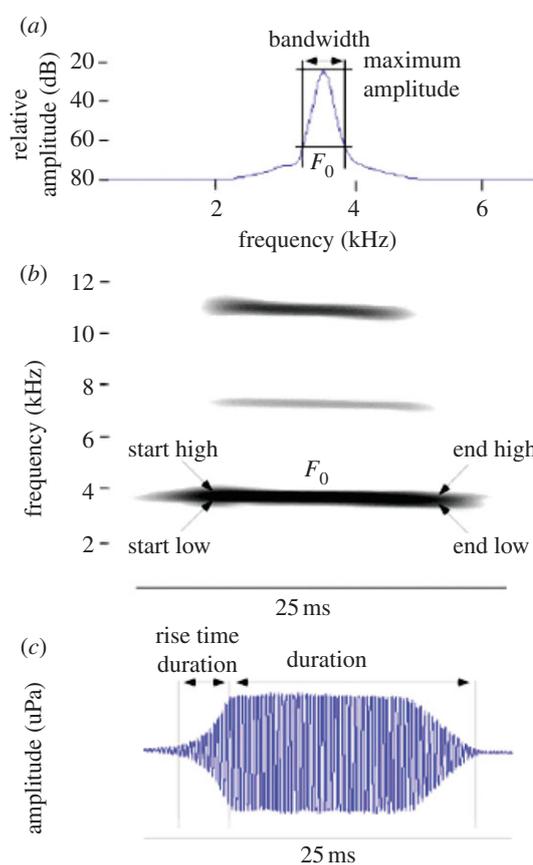


Figure 1. Illustration of the nine acoustic measurements made on the (a) spectrum (bandwidth, maximum amplitude and peak frequency), (b) spectrogram (start low frequency, start high frequency, end low frequency and end high frequency) and (c) waveform (rise time and duration) of yellow-bellied marmot alarm calls, used to study the heritability thereof. (Online version in colour.)

Fourier transformation size = 1024, overlap = 99.61%, filter bandwidth = 1066.32 Hz, frequency grid resolution = 3.07 Hz, clipping level = -80 dB; average spectrum: fast Fourier transformation size = 512, overlap = 99.8%, filter bandwidth = 533.16 Hz, frequency grid resolution = 86.13 Hz, clipping level = -80 dB). We then quantified nine quantitative measurements (figure 1): rise time and duration (measured from the waveform), F_0 peak frequency, F_0 maximum amplitude, F_0 bandwidth (from the spectrum: measured at the base of the peak when taking only the top 40 dB into account) and F_0 start high frequency at maximum amplitude (hereafter 'start high'), F_0 start low frequency at maximum amplitude ('start low'), F_0 end high frequency at maximum amplitude ('end high'), and F_0 end low frequency at maximum amplitude ('end low'); all measured from the spectrogram, which previous studies had shown to be individually distinctive [13].

We constructed a molecular genealogy where we used 12 microsatellite loci to determine maternity and paternity (details in [49,51]). Using the animal model [45,46], as implemented by ASREML [52], we decomposed the variance of alarm calls into its additive genetic, permanent environment (environmental effects on an individual's phenotype that are constant across repeated measures on that individual [53]), maternal environment (the effects on offspring phenotype that are shared by offspring of the same mother [53]), year and event (which reflects the consistency of calls during one recording event) components. We included sex and day of the year as fixed effects to control for sexual dimorphism and time variation. First, analyses were run separately for juveniles and a class that included yearlings and adults. This is biologically justified because yearling and adult alarm calls are more similar to each other than are juveniles,

which are quite acoustically distinctive, given their small body size [13]. We included an age effect as a fixed effect for the adult and yearling models to correct for potential differences between the age classes. We also fitted bivariate models that modelled juvenile and adult–yearling alarm calls as the two dependent variables. To test if variance components were different between the two age classes, a likelihood ratio test between bivariate models with and without constraints of equality of variance components for age classes was used. Residual and event covariance were fixed to 0 owing to the structure of the data. Year covariance was also fixed to 0 owing to convergence error. Additive genetic, permanent environment and maternal covariance were also set to 0 if one variance parameter was bound to zero in the univariate models. To ensure that differences in variance components between the two age classes were not due to scale differences, traits were standardized by their standard deviation after accounting for the fixed effect. Data are archived at www.eeb.ucla.edu/Faculty/Blumstein/MarmotsOfRMBL/data.html.

3. Results

Calling bout (i.e. event) accounted for a significant amount of variation in each of the measured variables (figure 1 illustrates acoustic measurements) both in juveniles and in yearlings and adults (table 1). For two variables, juveniles had significantly more variation explained by calling bout than did yearlings and adults (table 2). In juveniles, the permanent environment explained significant variation in four of the measured variables: duration, bandwidth, end high and end low (table 1), and in yearlings and adults, the permanent environment explained no significant variation in any of the variables. However, permanent environment estimates were not significantly different between juveniles and yearlings and adults (table 2). No significant additive genetic effects were found in juveniles, except for start low frequency (24.7%) (table 1 and figure 2*a*). Maternal environmental effects in juveniles explained significant variation in five variables: peak frequency (20.6%), bandwidth (10.5%), start high (17.5%), start low (17.1%) and end low (8.3%) (table 1 and figure 2*a*). By contrast, in yearlings and adults, significant additive genetic effects were found for all variables, except duration and end low frequency (table 1 and figure 2*b*). Only two of these variables, however, were significantly different as a function of age class (table 2). No maternal environmental effects were found in yearlings and adults (table 1), and four of the estimates were significantly different from juveniles (table 2).

The effects of fixed effects are reported in the electronic supplementary material, appendix S1. However, in juveniles, there was a difference between males and females for all traits except rise time, maximum amplitude and bandwidth, and there was a strong significant effect of day of the year in all the traits. For yearlings and adults, four traits (peak frequency, bandwidth, start high and start low) had significant sex differences. Day of the year affected call duration, maximum amplitude and start high frequency. Yearlings differed from adults for some traits: rise time, peak frequency, bandwidth, start high, start low, end high and end low.

4. Discussion

We found, for the first time, evidence of heritable alarm call attributes, but only in older marmots. By contrast, we found significant maternal effects only for juvenile calls.

While not all of these estimates were significantly influenced by age, estimates were significantly different from zero. The lack of significance between age classes in significant variance components may have resulted from the considerable variation in them as well as the relative effect size of ‘age’. Nonetheless, we have identified ontogenetic changes in the relative importance of heritability and maternal effects in alarm calls, and this result provides new insights into the potential utility and evolution of alarm calls.

Juvenile alarm calls have substantial and significant maternal environmental effects, but no significant heritability. The absence of heritability in juvenile alarm calls could be proximately associated with the strong effect of the day of the year. In their first year, marmots undergo rapid structural growth, and must put on two to three times their emergence body mass to have a good chance of surviving their first winter [55]. Vocalizations are influenced by physical structures, such as the size and shape of the vocal tract [56], suggesting strong acoustic consequences of rapid juvenile growth.

If maternal environmental effects in juvenile alarm calls were the result of vocal learning, perhaps to permit optimal transmission through the environment (i.e. the acoustic adaptation hypothesis [57]), then we would expect them to be retained into adulthood. Because they are not present in older marmots, our results suggest that we should look for something unique in the maternal environment and with a reversible effect as a putative mechanism.

From a proximate perspective, arousal level can influence both the probability of uttering alarm calls [58] and the structure of these vocalizations [59,60]. Juveniles born into particularly stressful environments (either because of social or predator stresses) might be exposed to more pre-natal and/or neonatal levels of glucocorticoids than juveniles born into less stressful environments [61]. Mammary glands are target organs for glucocorticoids, and thus they can be transferred to juveniles from their mother’s milk [62]. Variation in the pre-natal and neonatal stress environment is a putative mechanism to explain significant maternal environmental effects, after controlling for variation explained by maternal (and paternal) genetic effects. Thus, maternal stress could explain variation in juvenile alarm call structure.

Indeed, this maternal effect could be the mechanism that permits mothers to recognize their offspring despite the lack of significant heritable variation. Marmots of all ages also have individually distinctive vocalizations [13], and this provides another mechanism that would permit mothers to discriminate among their own from and other females’ pups. By contrast, other mammals (e.g. bats [39]) have a much more stable vocal structure over time.

From a functional perspective, the tighter link between environmental risks/stresses and call structure may be adaptive. Adults respond more to calls from juveniles than older animals [11], and marmots and meerkats respond more to calls with nonlinear acoustic attributes in them [63,64], acoustic features that may be produced under duress [65]. Thus, the variation produced by this putative maternal environmental mechanism may be adaptive in that it helps create calls that function to help juveniles born into a stressful environment (e.g. an environment with predators that stressed the mother) obtain what they need from older animals.

In older marmots, the absence of maternal environmental effects combined with the significant (and in some cases substantial) heritability of acoustic traits suggests that alarm

Table 1. Proportion of phenotypic variance after accounting for fixed effects (V_p) explained by additive genetic (h^2), permanent environmental (pe^2), maternal (me^2), event and year effects for alarm call structure. Significance of ratios was assessed using likelihood ratio tests. Significant variables are in italics. Standard errors generated by ASReml are presented in parentheses. Dashes (—) represent effects that were bound to zero.

trait	mean	V_p	h^2	pe^2	me^2	event	year
<i>juveniles</i>							
rise time (ms)	1.663	1.801 (0.110)	—	0.028 (0.069)	—	0.659 (0.072)***	0.021 (0.021)
duration (ms)	36.140	55.778 (4.447)	—	0.356 (0.072)**	0.0089 (0.031)	0.373 (0.06)***	0.065 (0.046)*
peak frequency (kHz)	3.534	0.157 (0.0167)	0.191 (0.159)	0.167 (0.116)	0.206 (0.084)**	0.341 (0.057)***	0.024 (0.029)
maximum amplitude (dB)	28.300	8.104 (0.405)	0.035 (0.034)	—	—	0.401 (0.039)***	0.026 (0.021)**
bandwidth (kHz)	1.174	0.148 (0.0124)	0.011 (0.063)	0.248 (0.071)***	0.105 (0.051)**	0.275 (0.048)***	0.085 (0.052)***
start high (kHz)	3.615	0.111 (0.0122)	0.176 (0.142)	0.131 (0.102)	0.175 (0.078)**	0.337 (0.057)***	0.088 (0.056)***
start low (kHz)	3.082	0.103 (0.0112)	0.247 (0.167)*	0.097 (0.113)	0.171 (0.08)**	0.299 (0.052)***	0.062 (0.043)**
end high (kHz)	3.344	0.175 (0.0129)	0.072 (0.089)	0.256 (0.086)*	0.067 (0.051)	0.361 (0.055)***	0.014 (0.022)
end low (kHz)	2.904	0.181 (0.0183)	0.049 (0.078)	0.255 (0.082)*	0.083 (0.052)*	0.331 (0.055)***	0.123 (0.067)***
<i>yearlings and adults</i>							
rise time (ms)	1.427	0.963 (0.0891)	0.326 (0.095)**	—	0.011 (0.06)	0.403 (0.055)***	0.011 (0.017)
duration (ms)	25.190	52.582 (6.75)	0.348 (0.206)	0.194 (0.168)	0.082 (0.088)	0.208 (0.036)***	0.033 (0.028)
peak frequency (kHz)	3.405	0.121 (0.0154)	0.436 (0.176)*	0.138 (0.149)	—	0.376 (0.058)***	0.009 (0.014)
maximum amplitude (dB)	27.520	5.956 (0.458)	0.176 (0.053)***	—	—	0.423 (0.047)***	0.062 (0.039)***
bandwidth (kHz)	1.000	0.0857 (0.00739)	0.158 (0.113)	0.168 (0.099)	—	0.246 (0.036)***	0.065 (0.039)***
start high (kHz)	3.598	0.102 (0.0132)	0.498 (0.163)**	0.113 (0.137)	—	0.308 (0.05)***	0.026 (0.022)*
start low (kHz)	3.091	0.107 (0.0136)	0.476 (0.160)**	0.128 (0.134)	—	0.280 (0.045)***	0.037 (0.027)**
end high (kHz)	3.292	0.122 (0.0129)	0.247 (0.144)*	0.159 (0.124)	—	0.385 (0.054)***	0.060 (0.04)**
end low (kHz)	2.869	0.109 (0.0115)	0.212 (0.148)	0.248 (0.135)	—	0.376 (0.053)***	0.037 (0.029)*

* $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

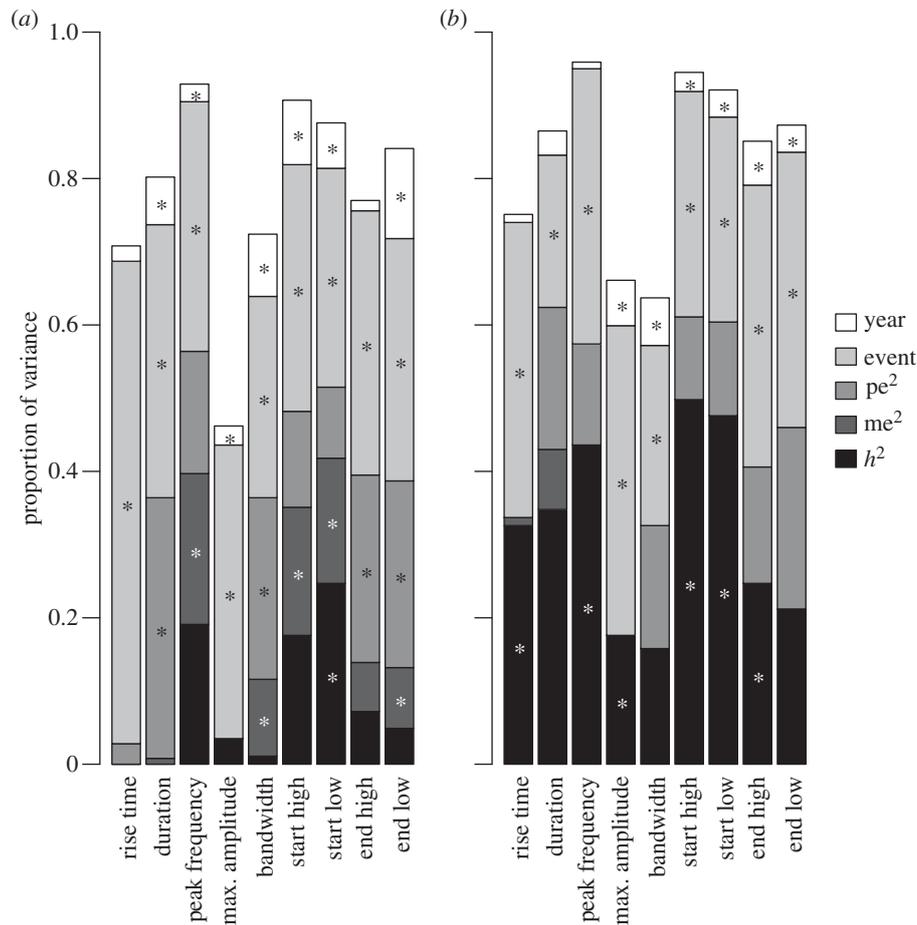


Figure 2. Proportion of variation explained by year, event, permanent environment (pe^2), maternal environment (me^2) and additive genetic (h^2), variation for alarm call structure in (a) juvenile and (b) yearling and adult yellow-bellied marmots. All estimates are from animal models fitted in ASReml. Significant ($p < 0.05$) effects are denoted by an asterisk.

Table 2. Likelihood ratio test and significance (n.s., non-significant) of the differences in variance components (additive genetic, h^2 ; permanent environmental, pe^2 ; maternal, me^2 ; event; and year effects) between juveniles and yearlings/adults for alarm calls structure in yellow-bellied marmots. Likelihood ratio tests were assessed between bivariate models with and without variance components constrained to be equal. Significance was assessed using 1 d.f.; however, it should be noted that this could provide a conservative estimate [54]. Significant values are in italics.

trait	h^2	pe^2	me^2	event	year
rise time (ms)	<i>6.679**</i>	0.140 (n.s.)	0.020 (ns)	<i>4.600*</i>	0.080 (n.s.)
duration (ms)	2.046 (n.s.)	0.226 (n.s.)	0.746 (ns)	<i>4.866*</i>	0.106 (n.s.)
peak frequency (kHz)	0.720 (n.s.)	0.020 (n.s.)	<i>6.207**</i>	0.340 (n.s.)	0.220 (n.s.)
maximum amplitude (dB)	<i>3.852*</i>	-0.008 (n.s.)	0.008 (n.s.)	0.212 (n.s.)	0.632 (n.s.)
bandwidth (kHz)	1.308 (n.s.)	0.402 (n.s.)	<i>6.054**</i>	0.280 (n.s.)	0.088 (n.s.)
start high (kHz)	1.400 (n.s.)	<0.001 (n.s.)	<i>6.012**</i>	0.460 (n.s.)	1.160 (n.s.)
start low (kHz)	2.140 (n.s.)	1.330 (n.s.)	<i>5.252**</i>	0.088 (n.s.)	0.244 (n.s.)
end high (kHz)	1.025 (n.s.)	0.241 (n.s.)	1.278 (n.s.)	0.578 (n.s.)	1.067 (n.s.)
end low (kHz)	1.118 (n.s.)	0.036 (n.s.)	2.170 (n.s.)	2.827 (n.s.)	1.308 (n.s.)

* $p < 0.10$, ** $p < 0.05$.

calls could be used to assess identity of the caller and kinship. Related marmots have calls that are more similar than non-related marmots.

If the changes in maternal effects with age classes suggested an absence of learning, as previously discussed, learning could nevertheless explain the observed ontogenetic pattern of heritability. If it took some time for animals to properly learn their calls, and they learned from relatives, resemblance with relatives would increase over time and

this would be seen in a greater heritability estimate in older animals. Future experimental studies would be required to demonstrate precisely what, if anything, was learned.

It is conceivable that alarm calls are important in kin recognition, but this initially seems unlikely, given that they are rarely uttered. Kin recognition in social context, such as mate selection or territoriality, could not reliably depend on alarm calls that were rarely uttered in response to predators. More probable is that identifying the relationship of the caller is

involved in caller reliability assessment [22]. The assumption here is that calls from relatives contain more potentially valuable information than calls from non-kin, perhaps because receivers can trust relatives. This is possible if animals are more likely to warn relatives than non-relatives [66]. While the assumption about the information content of calls from relatives versus non-relatives remains to be tested, our results identified a potential mechanism for kin recognition in alarm calls. Our work has thus opened a new avenue to investigate in the function and evolution of alarm calling.

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Genetic variation and heritability of ontogenetic trajectories was detected for trichome density only. These genetic pre-requisites for evolution, however, were not detected in the field, suggesting that environmental variation and phenotypic plastic responses mask any heritable variation. Finally, ontogenetic trajectories were found to be plastic, differing between shadehouse and field conditions for the same genetic families. Ontogenetic changes have been documented in the stamina and activity capacity of snakes (Pough 1977, 1978). Young (small) *Thamnophis sirtalis* and *Nerodia sipedon* exhaust far more rapidly than do adults of the same species. This differential stamina is directly correlated with ontogenetic changes in anaerobic capacity and aerobic scope in these animals. We probably eliminated post-natal maternal effects and common environment by moving siblings into identical individual cages the day after birth. Nevertheless it would be. Behavioural variation in natural populations. V. Mendelian models and heritability of a feeding response in the garter snake, *Thamnophis elegans*. *Heredity*, 51, 405-413. Benmtt, A. F. 1978.