Investigating the genetic architecture of conditional strategies using the environmental threshold model

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The threshold expression of dichotomous phenotypes that are environmentally cued or induced comprise the vast majority of phenotypic dimorphisms in colour, morphology, behaviour and life history. Modelled as conditional strategies under the framework of evolutionary game theory, the quantitative genetic basis of these traits is a challenge to estimate. The challenge exists firstly because the phenotypic expression of the trait is dichotomous and secondly because the apparent environmental cue is separate from the biological signal pathway that induces the switch between phenotypes. It is the cryptic variation underlying the translation of cue to phenotype that we address here. With a ‘half-sib common environment’ and a ‘family-level split environment’ experiment, we examine the environmental and genetic influences that underlie male dimorphism in the earwig Forficula auricularia. From the conceptual framework of the latent environmental threshold (LET) model, we use pedigree information to dissect the genetic architecture of the threshold expression of forceps length. We investigate for the first time the strength of the correlation between observable and cryptic ‘proximate’ cues. Furthermore, in support of the environmental threshold model, we found no evidence for a genetic correlation between cue and the threshold between phenotypes. Our results show strong correlations between observable and proximate cues and less genetic variation for thresholds than previous studies have suggested. We discuss the importance of generating better estimates of the genetic variation for thresholds when investigating the genetic architecture and heritability of threshold traits. By investigating genetic architecture by means of the LET model, our study supports several key evolutionary ideas related to conditional strategies and improves our understanding of environmentally cued decisions.

1. Introduction

The coexistence of discrete alternative phenotypes is widespread with intraspecific variation in morphology [1,2], physiology [3] and behaviour [4]. The degree to which alternative phenotypic expression reflects genetic or environmental variation falls on a continuum from genetic determination [5] to environmental influence [6], with the vast majority of cases somewhere between the two theoretical extremes. At one end of the continuum, are pure genetic polymorphisms [5], where a combination of alleles in one or a few loci determines the discrete phenotypic outcome. With the simplest genetic architecture for a discrete trait [7], genetic polymorphisms facilitated modelling under evolutionary game theory [8]. The name ‘alternative strategies’ [9] is used to describe such cases of complete genetic control of alternative phenotypes. At the other end of the continuum, are polyphenisms, where the differential expression of alternative phenotypes from a single genotype is dependent on environmental conditions...
In contrast to alternative strategies, the term ‘conditional strategy’ [11] is used when alternative phenotypes arise from developmental rules that are conditional on the environment (including other individuals), and/or even on other traits in the same individual. Owing to the predominance of environmental influence over genetic control, the genetic component is often overlooked when studying conditional strategies. However, genetic variation still plays a central role [12], because a ‘pure polyphenism’ or ‘pure conditional strategy’, with no genetic variance underlying the response to the environment, can only be manifested in clonal populations that lack genetic variation [13]. In fact, the role of genetic variation in polyphenisms [14–16] should be expected, because it allows adaptive evolution on ecological timescales in changing environments, keeping phenotypes close to their optimum [17]. Genetic variation in polyphenisms should also be expected from a mechanistic perspective, since a simple switch between two different phenotypes [10] is a complex process with many steps, such as sensing the environmental cue, contrasting it to an individual threshold, triggering a physiological/morphological response and developing the response. Hence, any genetic variation that affects any of these steps can impact the expression of a polyphenic trait.

The idea of polygenic genetic variation underlying the expression of dichotomous traits is at least 80 years old [18], and permeates the theory of threshold traits [19]. Such traits are believed to have their expression controlled by a hidden continuous variable called ‘liability’, which is subject to genetic and environmental factors. In the liability model, which alternative phenotype will be expressed by an individual depends on whether their liability exceeds a fixed threshold [19], and this model can be expanded to accommodate conditional strategies if the relative position of the threshold (compared to the distribution of liabilities) is a function of environmental cues [14]. This model has been termed the ‘environmental threshold model’ (hereafter, ET) [1,15], and it proposes that additive genetic variation for thresholds underlies variation in the sensitivity to the environment. Body size is often considered a trait under environmental influence and used as a proxy for the cue that influences the expression of alternative phenotypes. It is counterintuitive that an individual’s body size serves as a cue in a conditional strategy, because it is an inherent trait of that individual. However, body size is also the visible phenotypic expression of an underlying mechanism (e.g. an individual’s energetic state or its energy acquisition and allocation), and genes that influence this trait should segregate randomly with respect to the environments that they develop in. Therefore, for modelling purposes, body size can be considered along with environmental variation, and serves as a proxy to an individual’s status (sensus) [9].

From the ET model perspective, whenever two individuals experience the same value of the cue, and yet express different phenotypes, it is not possible to separate whether this results from individual differences in the genetic sensitivity to the cue or whether it results from non-genetic sources of variation, such as error in the measurement of the environmental cue, for instance. Therefore, separating genetic and environmental contributions to threshold variance has been limited. The few estimates of variation in threshold distributions have been very large, with the standard deviation of threshold distribution being as high as greater than 230% of the standard deviation of the cue (measured as status or body size; [20]). However, clearly in many systems the observable cue (for example, body size) may not be the cue being assessed by the individuals—or if it is—not measured in the same way (hormone titre versus linear dimensions or weight). Hence the cues we observe are at best proxies for what the organism itself uses as the cue. This means that the observable cue is correlated with a proximate cue that is unknown to the observer. This idea has been recently formalized in the latent environmental threshold (LET) model [21], where there are two underlying causes for different phenotypes being expressed under the same value of environmental cue: (i) genetic variation for thresholds, (ii) and non-genetic variation arising from underlying proximate sources, such as noise during the development of the structures that sense and integrate the response to the cue, or simply measurement error. By including the imperfect correlation between the observable (measurable) cue and the proximate (latent) cue, the LET model incorporates measurement error for the cue, in addition to the genetically determined threshold built into the ET model [15]. As genetic covariance among siblings is expected for the latter, but not for the former, it is possible to use pedigree information in the LET model framework to disentangle these two important sources of variation, and achieve a better estimation of the genetic parameters influencing the evolution of thresholds [21].

Here we investigate the genetic architecture of conditional strategies for male dimorphism in the forceps of the earwig Forficula auricularia. Male F. auricularia use their forceps in courtship [22] and fighting [23,24], with major males competitively superior to minors [23]. We examined the heritability of the conditional strategy, the genetic variance for thresholds and the genetic correlation between threshold and cue (status; using body size as a proxy). We also investigate the influence of the environment and the strength of the correlation between observable and proximate cues. We do so by gathering data from three natural populations, and coupling a quantitative genetics approach to an environmental (diet) manipulation. This study is one of the first uses of the LET framework to test the core concepts of the ET model, and we discuss the importance of generating better estimates of the genetic variation for thresholds, particularly when investigating the genetic architecture of threshold traits and estimating their heritability. Our study illustrates a promising approach to understanding polyphenisms and conditional strategies.

2. Material and methods

(a) Half-sib common environment

Final or penultimate instar F. auricularia were collected in June 2001 from under logs, stones and vegetation from the North Sea islands of Brownsman (BR), West Widesope (WWO) and East Widesope (EWO) in the Farne Islands group, Northumberland, UK. Approximately 1000 nymphs from each island were placed in plastic tubs (width: 300 mm, height: 300 mm, depth: 200 mm). The tub walls were painted with Fluon PTFE to prevent the earwigs climbing the walls and ventilated with a 150 x 200 mm hole cut in the lid that was covered with fine nylon mesh gauze. The nymphs were housed with four to five egg cartons for refuge. Nymphs were fed fish-based cat chow (kitty-kat) ad libitum and had ad libitum access to water from plastic 0.5 x 30 mm tubes filled with water and bunged with cotton wool.

Collected nymphs were returned to the laboratory and housed at 15°C in an LMS cooled incubator with 14 L/10 D cycle. Each day
after collection, the nymphs were checked for adults. New adults are white and clearly identifiable and do not mate when newly eclosed. Males and females from each island were maintained in separate tubs. At the beginning of October, male ‘sires’ were put with five virgin female ‘dams’ in a 50 × 50 × 30 mm clear plastic tubs with a piece of egg carton and ad libitum cat biscuits and water as above. These tubs were placed in a controlled temperature room at 10°C with an 8 L/16 D cycle. In this way, 137 sires were set up for the BR and EWO populations, while for WWO 111 sires were set up. At the beginning of November, dams were separated from the sires and placed individually into 25 mm Petri dishes that had been almost filled with a 75:25 mixture of damp commercial potting compost and sand. Female earwigs tend their eggs underground over winter and these Petri dishes provided a burrow like environment for them to lay their eggs in. The females in these Petri dishes were maintained at 5°C in the LMS incubator in complete darkness until April, when the temperature was increased to 10°C. At this time, we discarded females that had not laid, had infertile eggs or had died resulting in the loss of the clutch to mould.

Live nymphs were transferred to 50 × 50 × 30 mm clear plastic tubs with egg carton, ad libitum cat biscuits and water. Dam families were split between rearing tubs to reduce common environmental effects and were reared at an initial density of 10 nymphs or fewer per tub. Earwig nymphs were reared in the controlled temperature room at 15°C under a 12 L/12 D cycle to adulthood (six to eight weeks), when they were frozen. Subsequently, the pronotum width and length of the right forceps (as in [25]) were measured using an eyepiece graticule [25].

Earwigs were measured under a dissecting microscope with an eyepiece graticule [25]. The right forceps (as in [25]) were measured using an eyepiece graticule [25].

(b) Family-level split environment
These data are a new analysis of those previously published in [25], which can be used for detailed explanation of the methods. In short, 150 female earwigs and their clutches were taken from both BR and WWO in early April 1996 and placed into Petri dishes with compost as above and housed in a controlled temperature room. When the nymphs hatched (within weeks), 41 families from WWO and 58 families from BR were separated into four treatments, two diets and two densities (electronic supplementary material, table S2). Density (reared alone or in groups of eight in 50 mm diameter Petri dishes) was found to have very little effect on adult morphology [25]. The high-protein diet was goldfish ‘flake’, and the low-protein diet was porridge oats; and these diets had a dramatic effect on male morph. Earwigs were measured under a dissecting microscope with an eyepiece graticule [25].

(c) Classifying males into majors and minors
Furcula auricularia is generally considered male dimorphic on the basis of the strongly bimodal distribution of forceps length and the different allometric relationships of that trait with body size in large (major) and small (minor) males [26]. Here we classified males into majors and minors based on the approach proposed by Rowland & Qualls [27], but using skew-normal distributions [28]. We parametrized the distributions of forceps length for each population as mixtures of two skew-normal distributions, using finite mixture models implemented in the package ‘mixsmsn’ [29] for R v. 3.2.1 [30]. Next, the likelihood of belonging to each male morph was computed from the mixture models for each male based on their forceps length, and males were classified into the morph they were more likely to belong.

(d) The latent environmental threshold model
To make statistical inferences from empirical data, Buoro et al. [21] introduced a statistical framework (the Latent ET model) to assess conditional strategies by means of the ET model, the underlying core process. In the ET model, the individual dichotomous phenotype $Y_i$ is determined by the proximate cue $\eta_i$, which is compared to the threshold $\theta_i$:

$$Y_i = \begin{cases} 1 & \text{if } \eta_i > \theta_i \\ 0 & \text{if } \eta_i \leq \theta_i \end{cases}.$$

The cue $\eta_i$ varies among individuals as a function of the environment, while the threshold $\theta_i$ is considered an intrinsic property of the individuals, independent of $\eta_i$, meaning that the model is assumption-free regarding the correlation between the two. In the ET model, the individual threshold, the proximate cue and the parameters of their distribution are conceptual and non-observable quantities. However, using the LET model, these quantities can be inferred through (i) the relationship observed between the dichotomous trait $Y$ and an observable cue $X$ that is correlated with the proximate cue (i.e. a proxy) and (ii) the use of genetic relatedness among individuals (i.e. the pedigrees) in order to separate the threshold genetic variance from random noise in the proximate versus observable cue relationship. A detailed description of the model is given in the electronic supplementary material, A1.

The LET model hence estimates the individual hidden variables (or latent variables) of primary interest, i.e. the proximate cue and the threshold traits, and allows comparison of the distributions of threshold and cue between populations and treatments, as well as assessment of the genetic correlation $\rho$ between individual thresholds and cues. Buoro et al. [21] provides a simulation study supporting that the probabilities obtained with the LET model are reliable and robust to its assumed mechanistic model.

(e) Building the pedigrees
The pedigree for our ‘half-sib common environment’ experiment was entirely known due to the breeding design used. For the data from the ‘family-level split environment’ experiment, we are only certain of the identity of dams, and therefore the pedigree is only partially known. To cope with this issue, we simulated a realistic pedigree for each family using R v. 3.2.1 [30], corresponding to a mixture of full siblings and half siblings. The simulation procedure and associated R scripts are given in the electronic supplementary material, A2.

(f) Bayesian statistical inference
Parameter estimates of the thresholds and proximate cue distributions, and the individual thresholds and proximate cues ($\theta_i$, $\eta_i$), were obtained by means of a Bayesian approach using Markov chain Monte Carlo (MCMC) algorithms [31–33] as implemented in the JAGS software [34]. The JAGS code of our model and prior probability distributions for the unknown quantities that are not conditioned by any other quantity in the model are given in the electronic supplementary material, A3. We ran three parallel MCMC chains and retained 20,000 iterations after an initial burn-in of 5000 iterations. Convergence of MCMC sampling was assessed by means of the Brooks–Gelman–Rubin diagnostic [35]. Results are reported using medians and 95% highest density intervals (HDI) showing uncertainty in the estimation of parameters [36]. To make comparisons among treatments or populations, we assessed the credibility of a null value by examining the posterior distribution of the difference between parameter values (difference of means or standard deviations). If the null value does not fall into the posterior distribution (95% HDI), one can reject the null hypothesis. The probability that the null value falls into the posterior distribution of a given parameter $\Theta$ is reported as $Pr(0 > [\Theta | Y] > 0)$.
3. Results

(a) Half-sib common environment
The means of the thresholds ($\mu_0$) were clearly higher than the means of the proximate cues ($\mu_h$) for all populations (figure 1a; electronic supplementary material, table S3), leading to low frequencies of major males (figure 1d–f). The variances of the thresholds ($\sigma_0^2$) were slightly higher than the variances of the proximate cues ($\sigma_h^2$) for all populations (figure 1b), leading to high heritabilities ($h^2$; figure 1c; electronic supplementary material, table S3). The correlations between individual thresholds and proximate cues ($\theta_i$, $\eta_i$) were non-significant ($-0.06$ [HDI: $-0.14$; $0.01$] and $-0.05$ [HDI: $-0.04$; $0.14$] for the WWO and BR populations, respectively, figure 2). The correlations between

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Figure 1. Posterior distributions of the parameters of the LETM estimated for the male dimorphic forceps of the earwig *Forficula auricularia* from the islands of West Wideopen, Brownsman and East Wideopen. (a) Threshold ($\mu_0$) and proximate cue means ($\mu_h$), (b) their associated variances ($\sigma^2_0$ and $\sigma^2_h$) and (c) heritabilities $h^2$ based on 20 000 MCMC samples. The median and 95% highest density intervals are presented. (d,e) Each line ($n = 100$) corresponds to the distribution of thresholds (dark grey) and proximate cues (light grey) estimated from one randomly selected MCMC sample. The cumulative normal curve of tactic expression is also presented.
Figure 2. (a) Posterior distributions of the correlations $\rho$ between proximate cues $\eta$ and observable cues ($X$; light grey), and between proximate cues $\eta$ and thresholds $\theta$ (dark grey) for the earwig *Forficula auricularia* estimated for the dimorphic forceps of males. Populations were collected from the islands of West Wideopen, Brownsman and East Wideopen. The median and 95% posterior probability interval are presented. (b) Scatterplots of the proximate cues and observable cues (light grey) or thresholds (dark grey) values of each individual based on one (among 20 000) randomly selected MCMC sample. Ninety-five percent HDI are also presented (ellipses).
the observable cue $X$ and the proximal cue $\eta$ were high ($\rho > 0.7$; figure 2; electronic supplementary material, table S3).

Comparing populations, the distributions of the means for the thresholds ($\mu_\theta$) and proximate cues ($\mu_\eta$) of the BR population were clearly higher than those of the EWO and WWO populations (figure 1a; electronic supplementary material, table S3), as the 95% HDI of these differences did not include zero (electronic supplementary material, table S4). Surprisingly, the distributions of variances $\sigma_\theta^2$ and $\sigma_\eta^2$ were not different between populations (figure 1b), because their 95% HDIs included zero (electronic supplementary material, table S4). Despite the fact that populations differed mainly through the means of the threshold distributions ($\mu_\theta$) and the proximate cue distributions ($\mu_\eta$), all populations still expressed similarly low frequencies of majors (12% < $P[Y = 1] < 15%$; electronic supplementary material, table S1).

(b) Family-level split environment
The means and variances of the proximate cue ($\mu_\eta^2$ and $\sigma_\eta^2$) for the low-diet treatment were lower than those of the high-diet treatment for both WWO and BR populations (figure 3a,b; electronic supplementary material, table S5). The 95% HDIs of the differences of variances fell well above zero, and more than 99% of the credible values were greater than zero (electronic supplementary material, table S5). This suggests that the environmental variance was considerably reduced when exposed to a low diet, which led to a higher heritability ($h^2$) for the low-diet treatment than for the high-diet treatment in both populations (electronic supplementary material, table S5). The means of the distributions of thresholds $\theta$ were higher than those of the proximate cues $\eta$ for both diet treatments, and both populations, leading to low frequencies of major males, but especially so in the low-diet treatment (figure 3c,d). The correlations between individual thresholds and proximate cues ($\theta_i$, $\eta_i$) were again non-significant (0.02 [HDI: −0.11; 0.14] and 0.02 [HDI: −0.09; 0.13] for the WWO and BR populations respectively in the high-diet treatment; figure 4). The correlations ($\rho$) between the observable cue $X$ and the proximal cue $\eta$ were high ($\rho > 0.5$; figure 4; electronic supplementary material, table S5).
Figure 4. (a) Posterior distributions of the correlations $\rho$ between proximate cues $\eta$ and observable cues ($X$; light grey), and between proximate cues $\eta$ and thresholds $\theta$ (dark grey) for the earwig Forficula auricularia estimated for the dimorphic forceps of males with different diet treatments ('high' and 'low', see Material and methods). Populations were collected from the islands of West Wideopen and Brownsman. The median and 95% posterior probability interval are presented. (b) Scatterplots of the proximate cues and observable cues (light grey) or threshold (dark grey) values of each individual based on one (among 20 000) randomly selected MCMC sample. Ninety-five percent HDI are also presented (ellipses).
4. Discussion

Quantifying the variance underlying threshold responses to environmental cues has until recently been a difficult proposition. This is a gap in our understanding that pervades many or most of the subconscious ‘decisions’ that organisms make in response to their environment. Using the LET model, we derived precise posterior estimates of the parameters of interest from our quantitative genetics and diet manipulation experiments (figures 1–4; electronic supplementary material, tables S3–S5). From our half-sib breeding design, we showed that the three natural populations of *F. auricularia* studied differed mainly in their mean threshold, which was notably higher in the BR population. As the proximate cues were also higher in that same population, the frequency of majors was very similar across all populations. In the ET model, the evolutionarily stable tactic frequency is dependent on the distributions of thresholds and the distribution of cues, both being taken into account in determining how tactic fitness influences the evolution of thresholds [15]. Thus, selection can affect the distribution of thresholds through the fitnesses of the alternative tactics.

A common misconception arises in the interpretation of environmentally cued threshold traits when the ‘environmental’ cue is body size. The notion is that because body size is heritable and thresholds between tactics are also heritable—that body size cannot be treated as ‘environmental’—and furthermore that a genetic correlation between body size and threshold will inevitably evolve. The rationale behind treating body size as environmental however is that the environmental quality experienced by the organism is random with respect to whether the organism’s genotype disposes it to switch at (in this case) a smaller or larger body size. If this is true, body size and threshold should not become correlated. Similarly if the environment experienced has effects that ‘drop’ the phenotype onto either side of the genetic variation in the threshold—then the dimorphic trait is essentially environmentally determined. We see an example of the latter in our data—the diet manipulation yielded almost no major males in the low-diet treatments, and yet body size is a highly heritable trait within treatments and where the earwigs were reared in a common garden.

The fact that both thresholds and proximate cues were higher in the BR population initially seems to suggest that thresholds and cues are genetically correlated, such that evolutionary changes in the cue track changes in the thresholds. Evolutionary changes in body size do sometimes track changes in thresholds of alternative male phenotypes [37,38], and this could just be due to frequency-dependent selection acting on male morphs [39]. However, across numerous island populations of these earwigs, it has previously been shown that the frequency of male morphs in the population varies widely due to changes in the position of the threshold relative to the body size distribution [40], see also [41]). However, these are population comparisons, and as far as we know, no other study has directly tested the genetic correlation between body size and the threshold that underlies the dimorphism. The closest to such a test was a study on the environmentally cued pupal colour dimorphism in butterflies [42], where the authors found no evidence for a correlation between the preference for green or brown pupation sites and the tendency to produce green or brown pupae. Similarly, by manipulating habitat complexity, an artificial selection experiment with bulb mites found that male body size and threshold responded to selection in opposing directions; increased habitat complexity caused lines to evolve towards smaller bodies, whereas the thresholds for major morph expression evolved towards larger bodies, both changes causing a decrease in the frequency of majors [37].

From a mechanistic perspective, a strong genetic correlation between body size and threshold would mean that both traits jointly respond to selection as one, and the dimorphism would essentially be inherited as a genetic polymorphism (similar argument for environmental sex determination in [43]). Using pedigree information, we estimated these correlations to be extremely low, and most probably non-existent in *F. auricularia* (figure 2). This is important because it provides the quantitative genetic evidence in support of the observation that tactic frequency evolves to be very different across the natural populations through separate changes in threshold or body size [40].

The absence of the cue/threshold correlation reveals how populations can evolve from being dimorphic to monomorphic and vice versa. The characterization of the body size and threshold distributions shows that the variance in the threshold distribution extends beyond the variance in the proximate cue distribution (figure 1). Because the two are uncorrelated, there will be some large individuals which have thresholds that are beyond their achievable body size even in a good environment (there will be some small bodied ones but these are not detectable). These individuals are effectively canalized to be minor males. These phenotypes have been observed in the BR population as very large males that are minors [25]. Until now their phenotype could not be confidently attributed to the fact that they had not reached their threshold, rather than some phenotypic accident—whereas now we have evidence that the former does happen (figure 1). Similarly, the idea that thresholds can be present but lie beyond the cue distribution of the entire population is supported by our diet manipulation and serves to explain populations of earwigs, where fewer than 1 or 2% of males are majors [40]. The coexistence of conditional and canalized strategists in the same population has previously been supported by evidence from the defence dimorphisms of barnacles [2] and daphnids [13], and for alternative male phenotypes in bulb mites [16].

We showed that the different diet treatments affected the expression of the alternative phenotypes through the proximate cue. This result was consistent between the two populations studied, despite the fact that they again differed in the means of proximate cues and thresholds. In both experiments, we found relatively high correlations (\(\rho\)) between the observable cue (body size) and the proximate cue. These correlations ranged from 0.59 to 0.96 in our populations under common garden conditions and experimental diet manipulation. Exposure to an enhanced diet reduced these correlations (\(\rho = 0.59\) and 0.67) when compared to exposure to an inferior diet (\(\rho = 0.95\) and 0.96). However, this likely results from the fact that under the low-diet treatment males almost never reached a size that produced a major and only the very largest few did, so caution should be taken when interpreting these potentially inflated values of \(\rho\) in the low-diet treatment. Nonetheless, the values from our common garden experiment (\(0.77 \leq \rho \leq 0.88\)) are perhaps the most meaningful and indicate that body size, measured as pronotum width, is a reliable proxy to the unobservable proximate cue that triggers male dimorphism in *F. auricularia*. This result was expected of...
course, as the important role of body size for the expression of male dimorphic forces in earwigs has long been known [44]. But even when these correlations are strong ($\rho > 0.7$, for example), their complement ($1 - \rho$) is still biologically significant, as it reflects a variety of non-genetic sources of noise that so far have been ignored when estimating genetic variance for thresholds. We suggest that this is the reason why the variance of genetic threshold has been overestimated as being as large as approximately 105% of the variance in earwigs, and as large as approximately 237% of the variance in body size in Acarid mites [20]. By contrast, our results suggest lower genetic variance for thresholds (ranging from 50 to 100% of the total phenotypic variance; electronic supplementary material, table S4) in F. auricularia.

Our data support several key evolutionary ideas that can be applied to the genetic architecture underlying a myriad of environmentally cued decisions. In particular, more accurate estimates of the genetic variation of threshold traits will enable us to better predict their response to selection. Given that threshold variance and proximate cue variance are both terms in the formula for the selection differential on thresholds [15], they will affect the stable threshold distribution underlying a conditional strategy. These findings have broad application to the understanding of the evolution of environmentally triggered switches of any kind, from alternative morphological traits under sexual selection through behavioural switches (e.g. between dispersal and sedentary phases or aggressive and passive behaviour) through to developmental changes in life history (diapause, sexual mode) or morphology (trophic specialization).

**Ethics.** The collection of earwigs was approved by the national trust (UK).

**Data accessibility.** The data used in this study are available in Dryad: http://dx.doi.org/10.5061/dryad.32erp.

**Authors’ contribution.** B.A.B. and J.L.T. conceived and planned the study. J.L.T. collected the data. B.A.B. and M.B. contributed equally to analysing the data and preparing the initial manuscript. All authors contributed to the hypotheses put forward and tested, and to manuscript revisions.

**Competing interests.** We have no competing interests.

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