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CONTEXT-DEPENDENT INDIVIDUAL VARIATION IN FORAGING BEHAVIOUR AND PARENTAL CARE IN HOUSE SPARROWS

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CONTEXT-DEPENDENT INDIVIDUAL VARIATION
IN FORAGING BEHAVIOUR AND PARENTAL CARE
IN HOUSE SPARROWS

THESIS

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science in
Biology in the College of Arts and Sciences
at the University of Kentucky

By

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Lexington, Kentucky

Director: Dr. David F. Westneat, Professor of Biology

Lexington, Kentucky

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ABSTRACT OF THESIS

CONTEXT-DEPENDENT INDIVIDUAL
VARIATION IN FORAGING BEHAVIOUR AND
PARENTAL CARE IN HOUSE SPARROWS

Behaviors can exhibit a wide degree of plasticity depending on the environmental context in which they are expressed. Despite this, repeatable differences have been found among and within individuals across a wide range of taxa. For my thesis, I investigated individual differences in foraging and parental care. In the first experiment, I assessed house sparrows (Passer domesticus) for domain-generality among neophobia, habituation and associative learning as they are all responses to novelty. While the results of the study find individual differences in each of these contexts the conclusion supported separate mechanisms for each response (domain-specificity). In the second experiment, I examined how the loudness of brood begging vocalizations influenced parent trip time, food load size brought to the nest and the amount of time spent in the box. The results of this study found individual differences in trip time and the time spent in the box with regard to the initial five seconds of begging loudness during a parent's visit. Additionally, trip time was also influenced by the change in loudness within a visit. My findings reveal that individual variation may depend on the context in which individuals are measured.

KEYWORDS: Animal Behaviour, Individual Differences, Phenotypic Plasticity, Reaction Norm, Foraging, Parental Care

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November 20th, 2015
Date

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CHAPTER ONE

**The responses of foraging house sparrows
(Passer domesticus) to different types of novelty are mostly
domain-specific**

Introduction

Environmental change is common for most organisms, and such changes may be considered novel if an individual has never experienced them before (Sol et al. 2011). Organisms can respond to these novel changes in a variety of ways. One type of reaction is neophobia, a fear response individuals often have to novel stimuli (Greenberg and Mettke-Hotmann 2001; Brown 2013), the extent of which is measured as the change in behavior from a familiar environment to one with the novel stimulus (Ensminger and Westneat 2012). Upon repeated exposure to a novel stimulus, most organisms eventually habituate and return to a baseline response (Thompson and Spencer 1966; Groves and Thompson 1970; Rankin et al. 2009). Neophobia and habituation are thus linked because they can be responses to the same stimulus. Other novel stimuli can provide information about potential rewards leading to associative learning. As an example, pollinators are able to learn color and shape associations that relate to the reward of flower nectar content (Waser et al. 1996; Melendez-Ackerman et al. 1997). Associative learning, habituation, and neophobia are common responses to novelty (Martin and Fitzgerald 2005; Guillette et al. 2009; Ensminger and Westneat 2012), yet there is relatively little information about how they might be related.

While each of these responses is measured in distinct circumstances, associations among them may exist. The possibility of behaviors with a common link has led to a debate about the prevalence of domain-specific or domain-general mechanisms in the human behavioral ecology literature (Fodor 1983; Sternberg 1999; Barrett and Kurzban 2006). Domain specificity suggests a specific and separate mechanism for each behavior (Fodor 1983; Cosmides and Tooby 1994; Shettleworth 2000). Domain generality postulates that mechanisms producing behavioral responses in different contexts have some common elements and so may exhibit similar patterns of variation. These ideas are fundamentally related to recent research in animals on behavioral syndromes, or correlated suites of traits that show among-individual variation (e.g., Samuels 1998; Buller and Hardcastle 2000; Sih et al. 2004; Chiappe and MacDonald 2005; Dochtermann and Jenkins 2007). Domain-generality is thus a hypothesis about the existence of a behavioral syndrome, whereas domain-specificity implies that each response involves separate mechanisms and exhibits independent variation.

Behavioral syndromes occur when certain patterns of variation arise. Behavior is an example of a repeatedly-expressed trait, so it can vary both within and among individuals in a complex hierarchical fashion (e.g., Westneat et al. 2014). For a single behavior, the among-individual variation is called "personality" (Dingemanse et al. 2010; Nussey et al. 2007; Réale et al. 2010). It is useful to define a behavioral syndrome as distinct from personality, in which two behavioral traits

show patterns of covariation, typically among individuals (Sih et al. 2004). This among-individual covariation could exist either in overall mean expressions of two traits or covariance in the ways a particular trait responds to multiple different stimuli (i.e., among-individual covariance in plasticity to an array of stimuli). A behavioral syndrome/domain general mechanism for responses to novelty would thus be manifested in a covariance among individuals in their responses to multiple types of novelty.

Domain-general mechanisms to novelty seem likely. In the case of the response to novel objects, neophobia and habituation can occur in response to the same external stimulus. Individuals that are strongly neophobic might be expected to habituate differently than individuals who were weakly neophobic. In addition, personality has been documented for multiple behaviors related to novelty, such as in boldness, risk-taking and exploration (e.g., Bókony et al. 2012; Boogert et al. 2006; Verbeek et al. 1994).

The alternative hypothesis to domain-generality is that each response to novelty involves a different mechanism, perhaps with different inputs. Domain-specificity implies that complex forms of phenotypic plasticity may exist. Phenotypic plasticity, whereby the phenotype expressed by a genotype (or individual) varies across a range of environments (Woltereck 1909; Bradshaw 1965; Pigliucci 2001), is common throughout all organisms and all phenotypes ranging from gene regulation up through various complex individual behaviors (e.g., Pigliucci 2002). Complex, or multidimensional plasticity (sensu Westneat et al. 2009, 2014), occurs when multiple environmental factors affect a behavior. Domain specific plasticity in response to novelty could evolve if the impact of novelty varies across a complex mix of conditions (Heinrich et al. 1995; Shettleworth 2001; Mettke-Hofmann et al. 2006). Domain specificity is implicated if there are weak covariances in responses among individuals and the majority of behavioral variation, assuming minimal measurement error, occurs within individuals and within contexts. This would imply that individuals are responding flexibly to differences between contexts.

I tested the hypothesis that responses to several forms of novelty by captive house sparrows (*Passer domesticus*) would exhibit domain generality. House sparrows are a small songbird whose success as an invasive species has been attributed to their behavioral flexibility in foraging (Sol et al. 2002; Martin and Fitzgerald 2005). For example, wild house sparrows have learned to open automatic doors (Breitwisch and Breitwisch 1991), forage from the grills of cars (Simmons 1984) and pry bark off trees to find insects (Lowther and Cink 2006). Differences in neophobia and habituation between individuals and the sexes were found in one study (Ensminger and Westneat 2011). However, no study has investigated whether sparrows exhibit correlated responses to different forms of novelty. Our study measured the time to approach a food source and the time it took to feed in the contexts of a mild disturbance, novel objects, and a set of novel cues, each of which are situations free-living sparrows encounter in the wild. If responding to novelty was domain-general, then the measured traits should covary among individuals across contexts, implying a syndrome.

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Methods
Subjects and acclimation

      Foraging behavior of captive sparrows was studied in fall 2013 and 2014 at the University of Kentucky's Ecological Research and Education Center (EREC). This site contains 15 outdoor aviaries (3.66 × 2.44 × 2.44 m), each having a wooden frame with hardware cloth used to enclose them on all sides. Each aviary contained a tree for shelter and a platform where a food and water dish could be placed. The aviaries were grouped into twos or fours, connected by a center chamber with a window looking into each aviary. In each central window tripods and cameras were placed to allow for video recording of foraging behavior.

      Adult house sparrows were captured in seed-baited cage traps and mist nets at the University of Kentucky's Agricultural Experiment Station, located north of Lexington, KY (38°06′N, 84°29′W). Upon capture, unbanded birds were banded with a unique Fish and Wildlife band combination and up to three colored plastic bands so they could be easily identified by sight. If an individual had been previously banded, new measurements were taken and their band combination recorded. A total of 43 sparrows were tested, and all were returned to the site of capture within one month of being caught. Once a sparrow was captured it was transported to the EREC and placed in a single aviary. Each aviary included a tree, a sand dish, a water dish and a test platform; the platform consisted of two 23 x 23 cm boards with nine 3.5 cm diameter holes cut into the flat side of each board. The holes were arranged in a 3 x 3 pattern and each contained a 1.5 oz. plastic cup. Sparrows were given five days to acclimate to the aviary with food being randomized among the cups every other day.

Experiments

      The experiments were performed in a randomized order. All trials started with a one hour deprivation followed by an experimental trial (described below) in which video recorders were started and behavior was recorded for 1 hour. Finally, individuals were given easy access to food for at least 90 min. before another round was started. At most, three trials were completed per day. Each bird experienced three contexts; a set of baseline trials (n = 5) in which birds experienced their normal feeding set-up after being disturbed by the investigator while the boards were replaced and the camera was started, trials (n = 10) in which a novel object was presented on the feeding boards as well, and trials (n = 10) in which the birds were confronted with a novel cue to the location of food. I describe the details of the latter two below. The first baseline trial was the first trial a subject experienced, and then baseline trials were inserted between sets of 5 trials and at the end of all trials.

Novel Object Environment:

      I tested subject reactions to two objects that the birds had not previously experienced in captivity: a blue plastic cup (with weights inside) and a clear Mason jar. The novel object trials followed the same procedure as the baseline trials, but with the novel object placed in the center of the food board and with food located in the three wells on either side of the object. Objects were removed after each 1 hr trial. Subjects were tested with the same novel object for five consecutive trials but

the order of which novel object went first was randomized. The second novel object was also presented in 5 consecutive trials either after the first novel object (with a baseline trial in between) or after the 10 trials of novel cue association tests.

Novel Cue Association:

To assess differences in the abilities of adult sparrows to learn novel associations, I conducted a series of conditioning experiments using color associations. Individuals were first trained to locate food under covers (pieces of 4cm x 4cm pieces of paper attached to a disk of cardboard that fitted into the plastic cups). Sparrows were initially trained using white covers during which all cups had food. Training occurred in two stages. The first consisted of covers that were placed over half of each cup. Once individuals learned to feed in this manner, covers were placed completely over the cups. An individual was considered successfully trained when it had removed a least one cover and fed in two out of five trials. Individuals that did not complete the second training stage were not used in further analysis.

Once trained to flip covers off wells to access food, the association test used covers of green and purple, with four green covers covering food and fourteen purple covers over foodless wells. Each individual received this color association first, and was tested over five successive trials with food location varying across trials and all individuals receiving the same sequence of locations. After a baseline trial, subjects received with a set-up with the colors reversed (purple indicated food) for five trials. The location of food was similarly randomized across trials but not across individuals.

Video scoring

Videos were scored after all trials had been completed for a given season. All time variables were recorded in seconds unless otherwise stated. The scorer extracted the time the experimenter closed the aviary door after the food board was returned to the aviary, the time a bird first landed on the food board, the time a bird left the food board, visit number (which occurred each time the bird landed on the food board), and the time at which feeding first occurred.

Statistical Analysis

For each trial I extracted 'Latency to board', calculated as the elapsed time after the experimenter left the aviary until the subject bird first landed on the food board, and 'Latency to feed', calculated from the time a bird first landed on the food board until it fed. Both response measurements were log transformed. I used Proc Mixed and Proc Glimmix in SAS 9.3 (SAS Institute Inc., Cary, NC) to create linear mixed models to represent the phenotypic equation in order to assess patterns of variance among and within individuals in each context (Ensminger and Westneat 2012; Wetzel and Westneat 2014). Testing habituation and association learning required the use of trial number though initially one was subtracted from each trial so that the first trial was coded as 0. The phenotypic equation for how this appeared is:

$$Latency\ to\ board_{ij} = B_0 + ind_{0j} + (B_1 + ind_{1j})(Trial\ number) + e_{ij}$$

where the response (i.e. latency to board) of the jth individual at instant (i.e. observation) i is the sum of β_0 (the mean population response) and ind_{0j} (deviation of the jth individual's average response) plus $(B_1 + ind_{1j})(Trial\ number)$, the population slope and the individual's deviation in slope as measured over an environmental gradient (i.e. trial number), and lastly e_{ij}, the residual deviation from the reaction norm of the ith expression of individual j's phenotype (Dingemanse and Dochtermann 2013). In addition, the fixed effects of Julian date, start time, temperature and hours between trials were treated as covariates and mean-centered between individuals before being added to the model. This type of model was similarly created for the latency to feed. Individuals that never landed on the board were excluded from all analyses.

Our initial analysis of each dependent trait was designed to create a best fit model that accounted for the external sources of variance. In each model I included the among-individual fixed effects of sex, year, capture group number and the between mean-centered covariates. For tests involving a novel object, the object order and the object type were included, while the association test had an additional fixed effect of color order. Also included was the random effect of aviary. I used backward elimination to remove terms that had the smallest F-value and a p-value greater than 0.05. I then included the within-individual fixed effect of trial number and compared models with and without the random effect of individual identity using a likelihood ratio test (Pinheiro and Bates 2000; Zuur et al. 2009) to determine if there were significant differences between individuals in intercept. To test for among-individual variance in slopes, I first included the within-individual effect of the adjusted trial number, followed by backwards elimination to remove terms that had the smallest F-value and a p-value greater than 0.05, then used the likelihood ratio test to compare models with the random effects of individual intercepts and a model with the random effect of individual slopes plus the covariance between slope and intercept with df = 2.

To assess neophobia, I compared the behavior of subjects in baseline trials with their behavior in the first trial of each novel object presentation. Additionally, I coded *Object* with the baseline trials as -0.5 and the novel object trials as 0.5 so slopes would equal the difference between the two groups. The equation to assess neophobia appeared as:

$$Latency\ to\ board_{ij} = B_0 + ind_{0j} + (B_1 + ind_{1j})(Object) + B_f(Obj\ type) + e_{ij}$$

In this case the response (latency to board or time to feed) was measured across the environmental gradient of the presence or absence of an object. In addition, an estimate of any relevant fixed effect (i.e. object type) was added to the equation to test the population's response with B_f representing the estimate of each fixed effect.

I tested for two types of covariances to assess if subjects' responses to different kinds of novelty had elements in common. One type of covariance was that observed between the 'Latency to board' and 'Latency to feed' which was estimated within individuals and within the same context. For this analysis the covariance matrix looked like:

$$\left[Y_{LTB_{ijx}}, Y_{LTF_{ijx}}\right] \sim MVN(0, \Omega_{ind}): \Omega_{ind} = \begin{bmatrix} V_{LTB_{ijx}} & Cov_{LTB_{ijx}, LTF_{ijx}} \\ & V_{LTF_{ijx}} \end{bmatrix}$$

In this case the context (x) for individual (j) at instance (i) covariance matrix for two phenotypic traits is shown. Unlike in univariate models, multivariate models have individual responses that are not independent and thus have a variance-covariance structure (Ω_{ind}) that separate within-individual variance ($V_{LTB_{ijx}}$ and $V_{LTF_{ijx}}$) from covariance ($Cov_{LTB_{ijx}, LTF_{ijx}}$). Similar separation is done for residual deviation (Dingemanse and Dochtermann 2013). I ran these models for three contexts; the 5 baseline trials, the 10 novel object trials, and the 10 color association trials with and without the adjusted trial order variable as a covariate. I used a likelihood ratio test to test for significance.

I also estimated within-trait but across-context and among-individual covariances, using a multivariate mixed model in which the same responses measured in each context was treated as a different trait:

$$\left[ind_{LTFx}, ind_{LTFy}, ind_{LTFz}\right] \sim MVN(0, \Omega_{ind}): \Omega_{ind} =$$
$$\begin{bmatrix} V_{ind_{LTFx}} & Cov_{ind_{LTFx}, ind_{LTFy}} & Cov_{ind_{LTFx}, ind_{LTFz}} \\ & V_{ind_{LTFy}} & Cov_{ind_{LTFy}, ind_{LTFz}} \\ & & V_{ind_{LTFz}} \end{bmatrix}$$

This assessed how similar individual intercepts in 'Latency to board' and 'Board to feed' within each of the three contexts (x, y, or z) were relative to other individuals. Because I found little individual variation in slope (see Results), I focused these analyses on intercepts. Adjusted trial order was included in all models. Significance of the covariances for each response variable was tested against a model with these set at 0 using a likelihood ratio test with 3 df.

Ethical Note

The research for this project was conducted with approval by the University of Kentucky's Institutional Animal Care and Use Committee (protocol 2012-0948). The subjects in this study where held for a total of 1 month for testing purposes. To ensure birds were healthy, they were kept in large outdoor aviaries with ad lib food and water including minimal human disturbance. During the experiments, birds were only handled during the initial placement into the aviaries and capture for release at the site of initial capture. The length of time birds were deprived was short (1 hr) and they were allowed to recover for 90 min or more between trials with a maximum of three trials completed in a day. Any bird that could not feed from any of the experimental set-ups was removed from the experiment and given easy access to food.

Results

Average responses

Trial order reduced both latency variables in both novel object and novel cue contexts (Table 1, Fig. 1). In the baseline trials, the latencies in the first trial, which was the first trial overall that a bird experienced, were significantly longer

than in other baseline trials (*LTB*: (-0.55 ± 0.15, $F_{1, 139} = 14.06$, p= 0.0003); *LTF*: (-0.27 ± 0.12, $F_{1, 140} = 5.38$, p= 0.02).

I also found a large and significant increase in both latencies in response to the appearance of a novel object (*LTB*: (0.64 ± 0.11, $F_{1, 187} = 36.38$, p< 0.0001); *LTF*: (0.53 ± 0.10, $F_{1, 191} = 27.69$, p< 0.0001)). I found no effect of the type of novel object or the order of presentation. In the color association trials I found birds exhibited significantly longer latencies in the reversal set-up (in which purple indicated food) than in the initial color pattern (in which green indicated food) but only for 'Latency to board' (0.13 ± 0.06, $F_{1, 331} = 4.32$, p= 0.04).

Table 1.1: Population slopes measured across trial order for latency to board and latency to feed of captive house sparrows in three contexts

Response	Context	Estimate ± SE	F value	DF	P value
Latency to board	Baseline	-0.07± 0.05	2.48	136	0.12
Latency to feed	Baseline	-0.05± 0.03	2.69	140	0.1
Latency to board	Habituation	-0.09± 0.02	14.33	261	0.0002
Latency to feed	Habituation	-0.12± 0.02	21.01	244	<0.0001
Latency to board	Association	-0.05± 0.02	6.99	310	0.009
Latency to feed	Association	-0.12 ± 0.02	48.54	276	<0.0001

Figure 1.1: Box plots and estimated individual reaction norms for two measures of captive house sparrow behavior in two contexts over repeated trials. (A, B) The latency from the start of the trial to when the subject arrived at the board and (C, D) the latency from arrival at the board to first feed from the board. (A, C) show behavior seen during the novel object trials, lumping both objects and (B, D) during the novel cue trials combining both cue combinations.
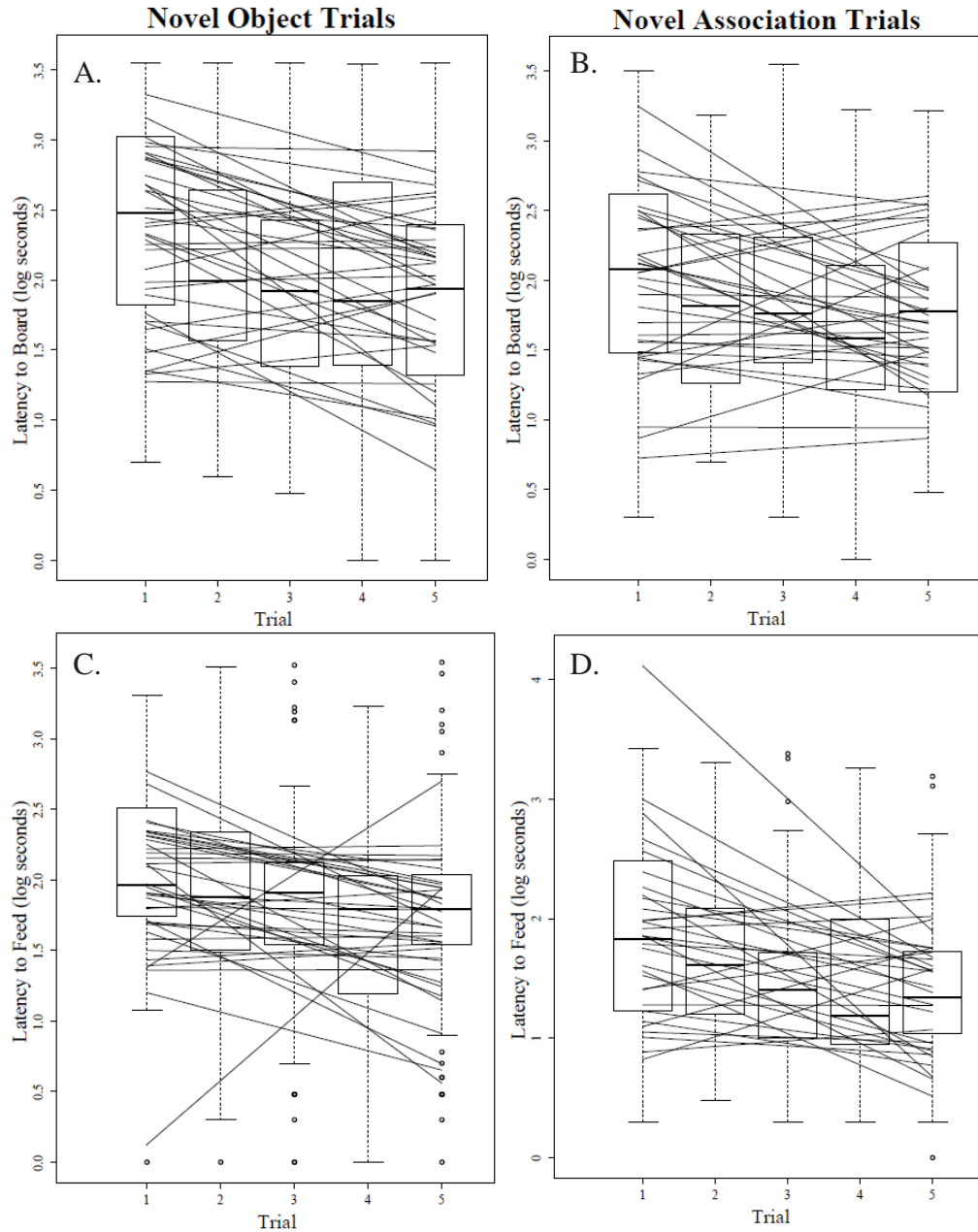
Among-individual variation within contexts

Within contexts and traits, the subject sparrows could exhibit among-individual variation in either intercepts (expected value at the first trial) or in slopes. I found significant variance in intercepts for both 'Latency to board' and 'Latency to feed' in the novel object and novel association trials. I also found significant among

individual variance in intercepts in baseline trials for Latency to feed (Table 2) but not Latency to board.

Table 1.2: Within context among-individual variance in intercepts determined as the random effect of individual in a mixed model.

Response	Context	Estimate ± SE	Chi-value[1]	DF	P value
Latency to board	Baseline	0.08 ± 0.04	24.6	1	<0.0001
Latency to feed	Baseline	NC	.	1	.
Latency to board	Neophobia	0.04 ± 0.04	1.9	1	0.17
Latency to feed	Neophobia	0.007 ± 0.02	0.2	1	0.65
Latency to board	Habituation	0.11 ± 0.05	12.1	1	0.0005
Latency to feed	Habituation	0.14 ± 0.05	32.6	1	<0.0001
Latency to board	Association	0.08 ± 0.04	23.8	1	<0.0001
Latency to feed	Association	0.4 ± 0.02	4.6	1	0.03

[1] From a likelihood ratio test

I also tested for among-individual variance in slope with respect to trial number within each of the three contexts (baseline, novel object, and novel cue). I found significant individual differences for just the latency to the board in the novel cue trials (Table 3). I also assessed slope for the transition from baseline to the first trials in each novel object test. I found significant among-individual variance in slope for both latency to board and the time from board to feed (Table 3).

Table 1.3: Within context individual differences in slopes

Response	Context	Estimate ± SE	Chi-value	DF	P value
Latency to board	Baseline	0.008 ± 0.01	2.5	2	0.29
Latency to feed	Baseline	NC	1.7	2	0.43
Latency to board	Neophobia	0.08 ± 0.04	24.6	2	<0.0001
Latency to feed	Neophobia	0.14 ± 0.05	32.6	2	<0.0001
Latency to board	Habituation	0.002 ± 0.005	0.2	2	0.9
Latency to feed	Habituation	NC	3.9	2	0.14
Latency to board	Association	0.005 ± 0.005	1.4	2	0.5
Latency to feed	Association	0.01 ± 0.009	2	2	0.4

Within-context covariances

I predicted that the two latency measures would covary positively within individuals, at the least because of similar effects of trial order on behavior. I found little evidence for within-context across trait covariance in the baseline and novel association contexts, even though trial order had a significant overall effect on both traits in the same direction in both contexts (Table 4). In the habituation context, latency to board and latency to feed were significantly correlated, although the effect was weakly negative and disappeared when trial order was included. In all other

contexts, including trial order reduced the covariances slightly, but did not alter significance.

Table 1.4: Within-context covariances between the latency of house sparrows to land on the board (LTB) and the latency from the board to feed (LTF).

Response	Context	Individual	Estimate ± SE	Z value	DF	P value
LTB v LTF	Baseline	Within	-0.001 ± 0.03	7.55	6	0.97
LTB v LTF	Baseline	Among	0.04 ± 0.02	1.69	6	0.09
LTB v LTF	Association	Within	-0.02 ± 0.02	0.80	6	0.42
LTB v LTF	Association	Among	-0.03 ± 0.04	-0.81	6	0.4
LTB v LTF	Habituation	Within	-0.05 ± 0.02	-2.29	6	0.02
LTB v LTF	Habituation	Among	0.05 ± 0.05	0.9	6	0.4

Across-context covariances

If responses to different types of novelty reflect a general mechanism, then individual differences within contexts should covary with those expressed in other contexts. Because I found few individual differences in slopes, I tested only the within-trait across-context covariances in intercepts. For latency to the board, a comparison of a model containing the three cross-context covariances (baseline-novel object, baseline-novel cue, and novel object-novel cue) explained significantly more variation than one without (-2 Res Log= 2978.09, χ^2 = 23.2, DF = 3, p< 0.0001). All covariances were low (<0.10). By contrast, a model with the covariances among contexts in latency from board to feed did not differ significantly from a model without those covariances (-2 Res Log= 2961.4, χ^2 = 6.5, DF = 3, p = 0.09) and two of the three values were < 0.05.

Discussion

House sparrows, like many species, respond to several well-defined types of novelty in their environment. The subjects in our study exhibited neophobia, a delay in approach to benign novel objects appearing suddenly near a traditional source of food. Our subjects also habituated to these objects over repeated exposure. They also learned to associate novel cues to the location of food and showed more efficient food-finding after repeated trials. Such responses are a regular feature of most animals that have been tested (Shettleworth 2001; Wasserman and Zentall 2006). Our goal, however, was to assess how individual differences manifest within and across these contexts.

I found significant among-individual variance in behavior (i.e., reaction norm intercept) for both behavioral traits in most contexts. Because both are latencies to approach and both exhibited significant increases when novelty first appeared, it may be appropriate to label what I have measured as evidence of individual differences in risk-taking or boldness. However, I did not find any evidence the two traits covaried within individuals, which is surprising if both represent a general attribute called boldness. Another possibility is that this represents differences in motivation that fluctuate on an intermediate time scale (i.e., over a few days). This

would explain consistent differences in behavior within several of the contexts in which all trials were done within a few days of each other and the lack of covariances across contexts.

I also found no evidence of individual differences in learning (i.e., reaction norm slope) in the two learning contexts, in which on average sparrows exhibited habituation to novel objects or associative learning to novel cues. I found weak evidence that latency to the board exhibited among-individual covariance across the three contexts—that is, individuals quick to the board tended to be quick to the board in each type of novel setting, but these cross-context covariances were quite low. Thus, our study of how house sparrows respond to several types of novelty revealed little support for a general mechanism and instead suggests domain–specific mechanisms to each type.

Our overall conclusion is based on the lack of significance in multiple statistical tests. Usually, there are problems in making inferences from not rejecting the null hypothesis of no effect, and since many of these tests focus on random effects (individual slope terms and covariances between contexts in random intercepts) known to require large sample sizes, I may have poor power to detect such effects. However it is important in this case to note the reason for poor power, which is the large residual variance in responses, typically over 50% of the variance. If high residual variance was due to measurement error, then our conclusion about domain specificity would be in serious jeopardy. However, both of our variables are timing variables extracted from video observations in which there is little ambiguity about timing. Measurement error due to scoring videos was low and repeatability was 99%. Thus the residual variance must come from variance in the true response of the subjects, which by definition must be due to plasticity in response to unmeasured variables. Thus the high residual variation is itself evidence of domain-specificity.

I found that in most cases of among or within contexts there was no significant covariance between the traits, suggesting that each behavior may describe different phenomena. This separation of such similar behavioral traits that occur in sequence is surprising given that latency to board and latency to feed would initially appear to describe how individuals behave towards perceived risk in our experiments. It is conceivable however that latency to board encompasses the majority of a risk response so that once an individual no longer perceives a high risk, other mechanisms or behaviors could be more influential. For example, metabolism, activity levels or other cognitive abilities may determine how quickly an individual feeds once they no longer fear a form of novelty (Leimar 1997; Shettleworth 2001; Houston and McNamara 1999). Individuals also exhibited cross context personalities in latency to board but not latency to feed, further suggesting separate mechanisms for each trait.

Within particular contexts, patterns of among-individual variance in intercepts and slopes were similar between the two traits. Both traits exhibited significant individual differences in neophobia, adding to a growing body of analogous findings within this population (Ensminger and Westneat 2012) and in other species (Echeverria and Vassallo 2008; Biondi et al. 2010; Mettke-Hofmann 2013). Oddly though, I found no evidence for individual differences in intercept in

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the transition from baseline to novel object (Wilson et al. 1994; Brown et al. 2007; Reale et al. 2007), which is surprising given that significant variance in intercept was found in both the baseline and novel object trials separately. A possible explanation is that individual responses to the presence of a novel object increased the variation in behavior, making differences in intercept harder to detect due to our low sample size (Ensminger and Westneat 2012; van de Pol 2012). Alternatively, as previously mentioned, what I have considered to be "boldness" may in fact be differences in motivation to feed, which are masked by differences in boldness when novel objects first appear.

Another interesting result was the lack of significant differences found in responses between novel objects. From the bird's perspective it may have appeared that both objects had similar parameters. Not much is known about what makes an object novel or which parameters of novelty are most important, though previous studies suggest that some measure of complexity and size elicit greater reactions to risk-related novelty (Berlyne 1950; Greenberg 1983; Heinrich et al. 1995; Mettke-Hofmann et al. 2006) while others have shown species capable of learning color, patterns, shapes and spatial cues (Shettleworth 2001; Wasserman and Zentall 2006). Reactions to novelty are also confounded by previous experiences, as seen by the significantly longer response to our reversed association learning trials, making clear assessments about responses to novelty difficult (Fox and Millam 2004; Fairhust et al. 2011; Feenders et al. 2011).

In summary, our results support domain specificity between neophobia, habituation and association learning as there were almost no significant realtionships among them. Cognitive mechanisms may underlie these differences where neophobia requires quick assessments of new types of novelty while habituation and association learning employ cognitive mechanisms, such as memory, necessary for repeated exposures to a situation (Greenberg 2003; Boogert et al. 2006; Biondi et al. 2010; Levy et al. 2010). While our sample size was relatively small I were still able to distinguish individual differences in mean responses and slopes for various behaviors though it is possible that additional individuals might allow for better clarification of the high residual variation. I also conclude that the relatively simple act of coming to a feeding site and then searching and finding food is likely composed of separate behavioral mechanisms. Unfortunately our design did not allow us to examine these distinctions in further detail though it does suggest that researchers must be cautious when interpreting composite trait such as the overall latency from the start of a trail to feeding. The potential of understanding the exact mechanism of these behaviors and how they may influence an individual's fitness in the wild would be an intriguing line of future study.

CHAPTER TWO

Loudness of brood begging influences variation in the
reaction norms of parent house sparrows (*Passer domesticus*)

Introduction

Parents in species that provision dependent young might be expected to benefit by attending to cues of offspring need and responding appropriately. In birds, for example, parents usually increase their visits as the nestlings' age and to larger broods (Royama 1966; Nur 1984; Breitwisch et al. 1986; Wright and Cuthill 1990; Clutton-Brock 1991), both of which affect nestling demand. Parents also vary considerably in their provisioning behavior within relatively short time frames when neither nestling age nor brood size has changed. Parents may assess both long-term and short-terms changes in nestling demand through cues provided by begging nestlings. Indeed, multiple studies have shown that postural or vocal signals produced by nestlings alter parent behavior (Bengtsson and Ryden 1983; Redondo and Castro 1992; McRae et al. 1993; Kilner 1995; Leonard and Horn 1998, 2001b; Wright and Leonard 2002).

This response of parents to nestling-provided cues is likely part of a complex behavioral reaction norm exhibited by parents. The behavioral reaction norm approach allows for the separation of population and individual differences in intercept and slope responses (Nussey et al. 2005; Smiseth et al. 2008; Dingemanse et al. 2010). For a single behavioral trait, the population intercept is a measure of the average response at the mean environment while the slope is the average change across the environmental gradient. Among-individuals, "personalities" occur when within-individual variation is insufficient to explain among-individual variation in intercepts (Dingemanse et al. 2010; Nussey et al. 2007; Réale et al. 2010). Slope variation (often arising from plasticity) is measured across an environmental gradient and can also vary among individuals more than can be explained by within-individual variation (Martin and Fitzgerald 2005; Nussey et al. 2007). Growing evidence suggests that both personalities and individual differences in plasticity exist for parental care (Hatch 2003; Schwagmeyer and Mock 2003; Anderson 2006; Nakagawa et al. 2007; Dor and Lotem 2010; Westneat et al. 2011).

To address these ideas I used house sparrows (*Passer domesticus*), a widespread songbird that is a year-round resident of human-modified landscapes (Anderson 2006). Additionally, males and females pair monogamously, exhibit biparental care and breed multiple times a season (Schwagmeyer and Mock 2003; Wetzel and Westneat 2014). Prior research on this species found they display plasticity in parental care towards brood size and nestling age (Nakagawa et al. 2007; Ringsby et al. 2009), with between-individual differences being found in response to the latter (Westneat et al. 2011). In particular, the biological basis for among-individual variation in feeding rate slopes with respect to nestling age has been unclear. Here I apply the reaction norm approach to assess the variation in offspring cues that might influence parental care reaction norms. Specifically, I

address three questions: (1) Do nestling vocalizations while begging provide information about nestling demand of potential use to parents? (2) Do parents appear to attend to components of nestling vocalizations during begging? (3) How are parent reaction norms influenced by nestling vocalizations?

Methods
Study site and population

This study was conducted on a nest box population of house sparrows in the summer of 2014 at the University of Kentucky's Agricultural Experiment Station, located just north of Lexington, KY (38°06´N, 84°29´W). The study site consists of agricultural and pastoral fields, and multiple barns used for stabling horses and storage. I monitored a total of 12 house sparrow nest boxes located on the outside walls of two barns. House sparrows in this study population breed continuously from March through August of each year, with each pair attempting one to six clutches per season and averaging five eggs per clutch (Westneat et al. 2009). Eggs hatch approximately 11 days after incubation and are fed by parents for 14 to 17 days following. House sparrows exhibit bi-parental care with both sexes providing food and defending nest boxes (Lowther and Cink 2006).

Parents were trapped with mist nests or seed-baited traps and banded with a numbered, metal USGS band and a unique combination of colored plastic bands so they could be recognized by sight. Starting in April, I checked each nest box in order to obtain the first egg date and the first hatch date. Once nestlings reached 10 days old they were banded and left undisturbed until they were 21 days old; on which the nest box was checked for fledging.

Video Recordings

Parental care data was collected from April through August 2014 with Panasonic SDR-S70 cameras. Recorder boxes were erected between 1 and 5 m to either side of nest boxes. Recordings occurred in two hour blocks every other day starting the day after eggs hatched until nestlings were 12 days old. A majority of the videos were performed in the morning and the brood was weighed before and after each recording. Videos were later scored for each visit by each parent and included the time the focal individual landed on, went in, came out, and left the nest box. From these scores I obtained 'Trip time' which was the time a parent spent away from the box, measured as the time an individual left the box until the time they landed on the box on the following visit, 'Time in box', taken from the time an individual entered the box until the time they exited, and Latency from last visit', obtained from the time a bird entered the box minus the previous visit's time of entrance, regardless of parent identity. Additionally, I quantified the 'Load Size' or amount of food a parent brought on each visit as the ratio of food to bill size (ranging from a bill volume of 0 to 2).

Audio Recordings

Nestling behavior was recorded simultaneously with parental care data using Olympus ME15 microphones plugged into Zoom H1 Handy Recorders. Recorders were placed in a straw bag and hung below the focal nest box on a nail.

Previous observations have suggested house sparrows are not significantly affected by objects beneath their nest box (Westneat and Wetzel obs.). Microphones were hidden in nesting material while nestlings were being weighed, in order to keep the microphone stationary and unnoticeable to parents. Three notes were also played at the beginning of every recording to help standardize among observations. To calibrate the nestling begging calls to the parental care videos a distinct noise such as a spoken word or clapping which was recorded on both devices. Once matched, ten visits from each parent were randomly selected. The first five intervals of each visit, five seconds per interval, were selected and maximum amplitude, a measure of loudness at the loudest frequency during the interval, was scored using Raven Pro v1.5.

Analysis

I used Proc Mixed in SAS 9.3 (SAS Institute Inc., Cary, NC) to integrate the data from each five second interval within a visit. I first created random intercept and slope solutions for each visit. Specifically, intercept values were calculated from a best fit line of all the intervals within a visit and then measured as the predicted measure of loudness at the first interval of a parent's visit. The slope estimated change in loudness across all intervals within a visit. The initial loudness and the change in loudness comprised the two begging variables for each parental visit.

I modeled the factors that might affect the two measures of brood begging. The model contained fixed effects of brood size, nestling age, latency from last visit and parent sex. Also included were the random effects of box identity and observation session. I then used backward elimination to remove terms that had the smallest F-value and a p-value greater than 0.05, although I kept brood size and nestling age to control for the confounding effects each may have on the measure of begging. Following this, total load size from the previous ten minutes, previous twenty minutes and previous thirty minutes were added independently to assess various timespans over which parental care behavior may have influenced nestling behavior.

Repeatable individual differences for parental care traits were examined by creating linear mixed models in order to assess patterns of variance for each trait (Westneat et al. 2011; Wetzel and Westneat 2014). Each model contained the time a trial started, the temperature, precipitation, the Julian date of first egg laid, brood size, brood age, parent sex and brood attempt number. Also included was the random effect of individual parent and observation number. As in the models of begging, I used backward elimination to remove terms that had the smallest F-value and a p-value greater than 0.05, but kept brood size and nestling age regardless to account for confounding effects each may have. I then inserted each begging component's intercept and slope response separately to assess their effects on the population level of parental care and as a random slope to test for individual differences.

Results

Begging behaviors

The maximum amplitude was expected to change across consecutive intervals (Figure 1) and with nestling age and nestling number. Additionally, if our

begging components indicated hunger, I expected significant effects of the amount of food brought to the nest and the latency from the last visit. The results showed that while loudness decreased across the intervals within a visit ($F_{4, 3234} = 29.92$, $p < 0.0001$) no measure of food or brood size had any influence on the initial loudness or change in loudness during a visit (Table 1). The only significant effect found was the positive effect of nestling age on the intercept values of max amplitude (Table 1).

Figure 2.1: Maximum amplitude decreases across intervals within the same visit.
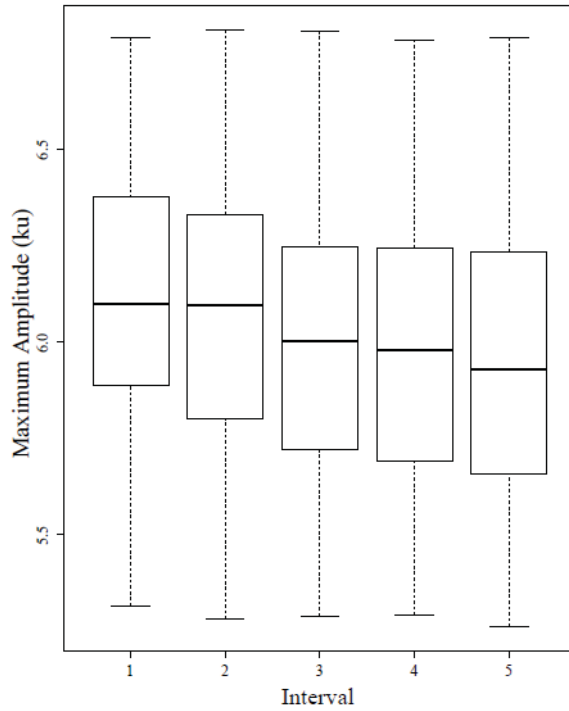
Table 2.1: Factors tested for their potential effects on the max amplitude of brood begging when parent house sparrows first arrived at the nest and for the change in maximum amplitude as the visit progressed.

Effect	Type	Estimate ± SE	F value	DF	P value
Brood size	Intercept	-0.01± 0.03	0.17	28.6	0.68
Nestling Age	Intercept	0.12± 0.01	157.37	35	**<0.0001**
Food 10 min	Intercept	0.02± 0.02	1.32	755	0.25
Food 20 min	Intercept	0.006± 0.01	0.29	716	0.59
Food 30 min	Intercept	-0.005± 0.01	0.28	627	0.60
Brood size	Slope	-0.0002 ± 0.002	0.02	41.2	0.89
Nestling Age	Slope	0.001 ± 0.0006	3.8	45.7	0.06
Food 10 min	Slope	-0.002 ± 0.003	0.55	279	0.46
Food 20 min	Slope	-0.003 ± 0.002	3.01	179	0.08
Food 30 min	Slope	-0.001 ± 0.001	0.60	150	0.44

Parent behaviors

Population parental care revealed that inter-visit interval was not significantly affected by the intercepts or slopes of the maximum amplitude of begging (Table 3). Trip time significantly increased with the date the first egg of that breeding attempt was laid (0.003 ± 0.001, $F_{1, 270} = 6.20$, p= 0.01) and decreased with nestling age (-0.02 ± 0.008, $F_{1, 67.9} = 5.25$, p= 0.03). There was no relationship with brood size (-0.02 ± 0.03, $F_{1, 74.6} = 74.6$, p= 0.41). Time spent in the box was significantly negatively influenced by the loudness of initial begging (Table 2), with brood size (-0.10 ± 0.04, $F_{1, 75.4} = 5.87$, p= 0.02), and nestling age (-0.09 ± 0.01, $F_{1, 106} = 53.52$, p< 0.0001). Lastly, the load size brought by parents was unaffected by either measure of nestling begging (Table 2), brood size (-0.002 ± 0.02, $F_{1, 40.6} = 0.01$, p= 0.93) or nestling age (0.01 ± 0.008, $F_{1, 79.5} = 2.51$, p= 0.12), though it did significantly decline the later in the day the recording was conducted (-0.00003 ± 0.000009, $F_{1, 67.8} = 7.75$, p= 0.007).

I found between-individual differences in trip time and in response to initial begging loudness and the change in loudness (Table 2). Time in box, on the other hand, only exhibited among-individual variance in response to initial loudness while load size was not affected by either measure of begging.

Table 2.2: Variation in house sparrow parental behavior with respect to the intercept and slopes of brood begging intensity.

Response	Response level	Begging*	Estimate ± SE	F-value	Chi-value	DF	P value
Trip Time	Population	Intercept	-0.12 ± 0.07	3.0		712	0.08
	Population	Slope	0.49 ± 0.49	1.03		812	0.31
	ID		0.02 ± 0.01		11.1	1	**0.0009**
	ID	Intercept	0.04 ± 0.03		7.6	2	**0.02**
	ID	Slope	0.54 ± 0.36		8.3	2	**0.01**
Food Load	Population	Intercept	-0.02 ± 0.05	0.25		351	0.62
	Population	Slope	0.01 ± 0.36	0		353	0.97
	ID		0.002 ± 0.003		0.3	1	0.6
	ID	Intercept	0.008 ± 0.01		1.7	2	0.43
	ID	Slope	NC		0	2	1
Time In Box	Population	Intercept	-0.26 ± 0.08	9.96		840	**0.002**
	Population	Slope	0.79 ± 0.56	1.98		824	0.16
	ID		0.02 ± 0.03		1.1	1	0.3
	ID	Intercept	0.08 ± 0.05		8.3	2	**0.01**
	ID	Slope	0.91 ± 2.6		3.9	2	0.14

* Intercept and slope refer to the expected begging loudness at the start of a visit (intercept) and the change in loudness over successive 5-sec intervals (slope) within a visit

Discussion

The goal of our study was threefold: assess whether nestling vocalizations

provide information about nestling demand that would be of use to parents, determine if parents attend to components of nestling vocalization, and examine the influence of nestling vocalizations on variation in parent reaction norms for provisioning. The three measures of parental care each represent a different component of use to addressing these questions. The time between trips and the food load size capture a measure of parental foraging effort for offspring while the time a parent spends in the box relates to aspects of brooding and the amount of time parent-offspring communication likely occurs. Furthermore, our results add to a growing body of literature that focuses on individual differences in parental care (Schwagmeyer and Mock 2003; Nakagawa et al. 2007; Westneat et al. 2011; Wetzel and Westneat 2014) and expands upon it by examining how each measure of parental care responds to variation in begging loudness both at the parent's initial contact with the brood (intercepts) and as loudness changed within the visit (slopes).

As might be expected, older nestlings begged more loudly. Thus begging loudness may be an additional cue of nestling age or at least correlates with changes in nestling age. This may be important especially for cavity nesting species where light levels are low, reducing visual information (Kilner and Davies 1998; Kilner 1999; Heeb et al. 2003). The lack of any relation to food amounts or brood size further suggests that loudness may be constrained only by lung capacity, which would change with nestling age.

The magnitude of changes in begging during a visit had no effect on parental behavior. I may not have had sufficient sample size to detect slight effects of this, but it does suggest that parents are likely mostly attending to the begging heard immediately upon arriving.

In response to louder initial begging parents spent less time in the box and tended to have shorter trip times between visits. While multiple studies have found that parents respond to nestling begging behavior within a given age (Clutton-Brock 1991; Kilner 1995; Budden and Wright 2001; Wright and Leonard 2002), these results provide detail regarding a specific timeframe that parents may attend to nestlings during a visit. The lack of begging dependence on food load size may have been due to food resources being variable and influenced by factors outside of an individual's control or potentially the quality may be more important than the quantitative measure we used.

Individual differences in parental care were found in some measures in response to begging loudness. The time spent in the box and the time between trips both exhibited among-individual differences in response to the initial loudness of begging. In addition, trip time also exhibited individual differences in response to the changes of loudness across the first twenty-five seconds a parent was in the box. These results suggest that individual parents respond differently to the same level of initial begging as well as the change in loudness for measures of trip time. One possible explanation for these differences could be parents attending to different begging cues (Smiseth et al. 2008). While our study focused on one measure of nestling begging behavior there are others cues that have been correlated with different measures of nestling condition or need that parents may use (Price et al. 1996; Leonard and Horn 2001a; Budden and Wright 2001). Alternatively, parents may have different internal states that may or may not

change slowly, thereby influencing their response to nestlings. For example, sex, age or previous experiences may influence individual plasticity in parental care (Curio 1983; Cluton-Brock 1991; Forslund and Part 1995; Kilner 2002; Quillfeldt et al. 2004; Ardia 2007; Angelier et al. 2007; Gladbach et al. 2009). As the data for this study are based mostly on a single nesting attempt with a relatively small number of individuals, prior experience or age effects could not be tested. While these results provide a clearer understanding of how parent-offspring communication occurs, there are still areas for further development. Specifically, it would be interesting to incorporate additional measures of nestlings and their begging behavior to understand more about the information being conveyed as well as the timeframe over which parents may be attending.

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PUBLICATIONS
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Moldoff, D and Westneat, D. *The responses of foragers to different types of novelty contain both general and specific components.* (in prep)

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