Food, sex and predators: animal personality persists with multidimensional plasticity across complex environments

Andy Dosmann*, Jill M. Mateo

University of Chicago, Committee on Evolutionary Biology, Chicago, IL, U.S.A.

The payoffs of an individual’s behaviour vary with changing environmental conditions. Animals often modify their behaviours according to those environmental conditions (i.e. plasticity), but also retain consistent individual differences across environmental change (i.e. personality). These patterns of behavioural variation are often measured with respect to a single environmental variable, which raises the question of how individuals respond to change in combinations of environmental variables, and whether individual differences in behaviour persist across change in multiple variables. Furthermore, an individual’s amount of plasticity in response to a change in one environmental variable may or may not be repeatable across change in a second environmental variable. To answer these questions, we experimentally manipulated combinations of mating, foraging and predation risk to determine their effect on the antipredator behaviour of male Belding’s ground squirrels, *Urocitellus beldingi*. We found that the combination of environmental variables had an interactive effect on antipredator behaviour, but among-individual variation persisted along with within-individual variation in behaviour. The plasticity of squirrels’ responses to change in one environmental variable, such as change in antipredator behaviour from high to low predation risk, was repeatable when measured in a mating environment and foraging environment, and vice versa. These results demonstrate patterns of behavioural variation across complex environments such as animals encounter in nature, and point towards the benefit of addressing greater environmental complexity in studies of animal behaviour.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

When animals exhibit consistent individual differences in behaviour over time and across environmental change, we refer to this as displaying personality or a behavioural syndrome (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). This among-individual variance contrasts with individuals’ behavioural flexibility in response to environmental change, known as behavioural plasticity (Dingemanse, Kazem, Réale, & Wright, 2010; Pigliucci, 2001; West-Eberhard, 1989). Understanding how personality and plasticity contribute to behavioural variation is a primary endeavour of animal behaviour research (Dingemanse et al., 2010; Sih et al., 2004; Stamps & Groothuis, 2010). A number of studies have found that a wide range of species display personality as well as plasticity to environmental variables such as temperature, experience and predation threat (Biro, Beckmann, & Stamps, 2010; Briffa, Rundle, & Fryer, 2008; Martin & Réale, 2008). These results call for studies of animal personality and behavioural plasticity addressing greater environmental complexity.

In natural environments, an individual’s response to one environmental variable may vary depending on the level of other environmental variables. To date, we know of only one study (Westneat, Hatch, Wetzel, & Ensminger, 2011) that assessed personality alongside the plasticity of a trait in response to change in multiple environmental variables, known as multidimensional plasticity (Westneat, Stewart, & Hatch, 2009). Brood size and nestling age have an interactive effect on parental provisioning behaviour of individual house sparrows, *Passer domesticus*, but there is also substantial among-individual variation of provisioning behaviour across variation in those environmental variables (Westneat et al., 2011). Furthermore, as multiple environmental variables fluctuate over time, a plastic response to one environmental variable, such as temperature, may or may not be repeatable at different levels of a second environmental variable, such as predation threat. In other words, is behavioural plasticity repeatable when a different environmental variable also changes? Here we experimentally manipulated combinations of multiple environmental variables in Belding’s ground squirrels, *Urocitellus beldingi*, to answer whether multidimensional plasticity persists with
animal personality, and whether plastic responses of individuals are consistent. Additionally, we compared results from models incorporating individual environmental variables separately to models incorporating multiple environmental variables and their interaction to highlight potential differences among multidimensional plasticity and traditional, unidimensional approaches to plasticity.

Belding’s ground squirrels are social rodents that are preyed upon by aerial and terrestrial predators (Mateo, 2007). They use their burrows as safe refuge, but forage and mate aboveground. Thus, individuals that are less risk averse, or bolder, are more likely to spend time aboveground relative to individuals that are more risk averse, or shy. The balance between risk and reward outside the burrow creates expectations that squirrels’ refuge use should vary as that balance shifts. We expect greater refuge use when predation threat is high versus low. Also, we expect greater refuge use in a foraging context versus a mating context, due to the greater evolutionary payoff of a potential mate over that of a potential meal. However, that prediction is predicated on individuals not being substantially food deprived, which will sometimes be the case in the field. An individual with low nutritional status would be expected to spend less time in the refuge in the foraging context than in the mating context. Because U. beldingi repeatedly measured refuge use of squirrels experiencing combinations of mating, foraging and predation risk environments to address three hypotheses. First, we hypothesized that the refuge use of squirrels shows multidimensional plasticity, which would be indicated by an interactive effect of environmental variables on refuge use. Second, we hypothesized that squirrels show consistent individual differences in refuge use across the manipulated combinations of environmental variables; that is, a relatively bold individual in one situation (combination of environmental variables) would also be relatively bold in another situation. Significant among-individual variance would support this hypothesis. Finally, we hypothesized that repeated expressions of plasticity to one environmental variable, such as predation risk, will show consistent individual differences across multiple environmental contexts, such as foraging and mating contexts. The field of animal personality aims to describe more comprehensively the behavioural variation of populations, and this experiment will help clarify how behaviours vary across complex, more realistic environments.

**METHODS**

**Animals**

Belding’s ground squirrels are social, diurnal rodents that inhabit the eastern Sierra Nevada and southern Cascade mountain ranges in California and Oregon, U.S.A. (Sherman & Morton, 1984). They hibernate each winter and are active between April and September each year. Their mating season is restricted to the first few weeks of the active season (Sherman & Morton, 1984), and the rest of the active season is primarily devoted to foraging to gain weight for the next winter hibernation. Due to the nature of the experimental manipulation of mating environment (see below), and the remarkably short oestrus of female squirrels (<6 h/year; Sherman & Morton, 1984), we only tested male U. beldingi. We measured antipredator behaviour of U. beldingi in a refuge use test. We emphasized on refuge use as an antipredator behaviour because it capitalizes on the balance between costs of differing predation risk and differing benefits of foraging and mating. The test consisted of a 122 × 122 × 61 cm arena built of wood, covered with a wire top and lined with an acrylic floor to facilitate cleaning and minimize residual squirrel odours across tests. An artificial burrow system in the centre of the arena provided a refuge similar to burrows in nature. The interconnected burrow system had three openings to facilitate access from anywhere in the test arena. We transferred each squirrel from its home cage to a Tomahawk live trap (Tomahawk Live Traps, WI, U.S.A.) and released it into the test arena from the trap through a door in the arena wall. Each test lasted 10 min, which pilot work in U. beldingi and studies of boldness and antipredator behaviour in other species indicates is a sufficient amount of time (e.g. Bell & Stamps, 2004). The novelty of the arena may have affected squirrels’ behaviours, but during the tests squirrels moved normally around the arena, including throughout the artificial burrow system. We measured the proportion of time they spent inside the refuge as an easily scored and clearly interpretable variable of antipredator behaviour, as more time in the refuge indicates stronger antipredator behaviour (Brieff et al., 2008; Rands, Cowlishaw, Pettifor, Rowcliffe, & Johnstone, 2003; Sih, Kats, & Maurer, 2003). To minimize observer effects we videotaped tests and scored them later blind to squirrel identity and treatment.

**Environmental Manipulations**

Olfaction is a primary sensory modality of U. beldingi (Mateo, 2009), so we used odours to manipulate foraging and mating environments. We used odours from oestrous females to simulate a mating environment and odours of a favourite food to simulate foraging environment. Although mating and foraging contexts are not strictly different levels of a single environmental variable, here we treated them as such. The natural history of U. beldingi supports
Experimental Design

We obtained four measurements of refuge use for each squirrel, one in the mating context and high predation risk, one in the mating context and low predation risk, one in the foraging context and high predation risk, and one in the foraging context and low predation risk. Treating high/low predation risk as two levels of one variable and mating/foraging as two levels of another variable makes our experimental design a $2 \times 2$ factorial with repeated measures. We chose this design to mimic natural situations that male U. beldingi encounter and to quantify multidimensional plasticity and personality across a tractable set of environmental manipulations. We conceptualized the two levels of each variable as two points along an environmental gradient, such that the mating and foraging treatments, and high and low predation risk treatments, were treated the way one would treat temperature manipulations of 26 °C and 29 °C (e.g., Biro et al., 2010). Additional trials as controls (e.g. no scent, scents of nonoestrous females, Frisbee paired with a nonpredator bird call) would have provided added clarity and support regarding the impact of the treatments. However, our design adheres to the standard set in the behavioural syndromes and personality literature of comparing between levels of context by (e.g. voracity of Doleristes triton in a mating and foraging context; Johnson & SiH, 2005) and provides a clear quantification of the multidimensional plasticity and personality of squirrels’ refuge use.

To obtain the four measurements of refuge use for each squirrel, we performed the test of refuge use described above on two separate test occasions. Each separate test occasion measured refuge use twice, once under high predation risk and once under low predation risk. On one test occasion, squirrels were presented with the mating odour treatment, and on the other occasion they were presented with the foraging odour treatment. In 2009, we tested 14 male squirrels. However, the order of foraging and mating manipulations was not counterbalanced. In 2010, we tested an additional 13 males, this time with a balanced order. When order was properly balanced in 2010, squirrels showed no order effects across test repetitions in both the high predation risk environment (paired $t$ test: $t_{12} = -0.82$, $P = 0.43$) and low predation risk environment ($t_{12} = 0.99$, $P = 0.34$). Because this difference was not significant, we combined data from both years for analysis. In our data collection set-up, low predation risk always preceded high predation risk, because the time period following the aerial predator stimulus was defined as high predation risk. So while we were able to balance the order of the odour treatments, there was an order confound for the predation risk treatment. In a similar test apparatus, many squirrels became habituated and unresponsive to four repeated test occasions in a short period. This prevented an experimental design that balanced the order of all experimental combinations across separate test occasions. We acknowledge that this design shortcoming hampers interpretation of our results. To clarify our interpretations of results in light of this potential effect, we measured within-test order effects in a separate sample of 11 male squirrels. We compared refuge use in the first 5 min of the test versus the last 5 min, but with no predator stimulus. If squirrels spend more time in the burrow during the last 5 min due to an order effect, then the order effect will be confounded with our prediction of refuge use with respect to predation risk, preventing interpretation of the treatment effect. However, an order effect in the opposite direction, or no order effect, will allow interpretation of greater burrow use in the high predation risk treatment as due to the effect of the predator stimulus. We found significant differences in refuge use, but the effect was in the opposite direction of our prediction for antipredator behaviour in high and low risk manipulations (paired $t$ test: $t_{10} = -6.39$, $P < 0.001$). Because our
predicted treatment effect is directional (greater refuge use under high predation risk), the order effect is not a confound, but it does prevent clear interpretation of effect size.

**Statistical Analysis**

We used linear mixed-effects models to assess behavioural plasticity and animal personality of antipredator behaviour. We conducted our statistical analysis in R 2.15.2 using the lmer command in the lme4 package. We arcsine transformed proportion of time in the refuge to improve how the residuals of the models fit normality and homogeneity of variance assumptions. We also standardized those values to clarify interpretation of coefficients (Schielezeth, 2010). Residual plots confirmed that the models using arcsine-transformed data did not violate model assumptions.

Warton and Hui (2011) recently advised against arcsine transformation for proportional variables such as ours, recommending a binomial model using counts of successes and failures to comprise the proportion. However, when we used binomial models, residuals did not meet homogeneity of variance assumptions and were overdispersed, whereas the normal model using arcsine-transformed data had well-behaved residuals, so we report those here. Mixed-effects models allow assessment of plasticity through evaluation of the fixed effects terms, in this case the environmental manipulations, and they allow the assessment of personality through evaluation of a random term representing individual identity (Dingemanse et al., 2010). Because each of the environmental variables is a two-level categorical variable, plasticity is the difference between values at those two levels rather than a true slope (Ensminger & Westneat, 2012). Therefore, as advocated by Ensminger and Westneat (2012), we coded mating and foraging treatments as \(-0.5\) and \(+0.5\), and coded low predation risk and high predation risk treatments as \(-0.5\) and \(+0.5\). This produces results that can be interpreted as slopes with the intercept centred at zero.

For the sake of comparing multidimensional plasticity to traditional unidimensional approaches, we ran multiple sets of models. We first ran mixed models evaluating personality and plasticity across each of the environmental manipulations separately, coding the particular environmental manipulation as a categorical fixed effect with two levels. Then we ran a full model including both environmental variables and their interaction as fixed effects. In each model, we included squirrel identity as a random intercept term and environmental manipulations as random slope terms (Schielezeth & Forstmeier, 2009). To test for significance of the random effects terms, we performed a likelihood ratio test between a model with the particular random effect and a simpler model without it, while maintaining the fixed effects structure (Crawley, 2007). We used the package RLsRsim using the exactLRT function to calculate accurate P values when comparing models with a single random effect to models with no random effect (Crainiceanu & Ruppert, 2004). We obtained test statistics and P values for fixed effects after standardizing the response variable (Schielezeth & Forstmeier, 2009). We calculated degrees of freedom using traditional ANOVA methods on our sample of 108 observations on 27 individuals, which was appropriate since we had equal sample sizes across treatments.

We also tested whether male *U. beldingi* show consistent individual differences in plasticity across a secondary environmental variable. We wanted to explicitly test whether the individuals with greater plasticity of refuge use across predation risk treatments in the mating environment also had greater plasticity across predation risk treatments in the foraging environment. In other words, we tested for consistent individual differences in plasticity across environments. To test this, and the converse that individuals that showed greater plasticity across mating and foraging treatments in the low risk environment also showed greater plasticity when in high risk, we calculated difference scores. A difference score is a simple way to quantify plasticity across two discrete levels of an environmental variable (Pigliucci, 2001). For example, we subtracted refuge use in the high risk manipulation from refuge use in the low risk manipulation. We calculated one difference score in the foraging odour treatment and another difference score in the mating odour treatment. Then we calculated the Spearman correlation between these two variables, as the difference scores were not normally distributed. To determine whether individual differences in plasticity to mating and foraging contexts were consistent across high and low predation risk, we subtracted refuge use in the mating environment from refuge use in the foraging environment for both high and low predation risk treatments and then calculated the Spearman correlations between the two variables. Our approach is similar to Morand-Ferron, Varennes, and Giraldeau (2011), except we did not use absolute value scores for plasticity because in our experimental set-up, the direction of plasticity is biologically relevant.

**RESULTS**

**Plasticity of Antipredator Behaviour**

On average, male *U. beldingi* spent about one-third of the test period in the refuge (mean \(\pm\) SD proportion of time in refuge \(= 0.34 \pm 0.29\)). Individuals changed their refuge use between environmental manipulations, with squirrels showing more refuge use in the high predation risk treatment than in the low risk treatment (Fig. 1a), and more refuge use in the foraging context than in the mating context (Fig. 1b). However, there were differences between unidimensional and multidimensional plasticity. When only main effects were included in the unidimensional models, squirrels significantly increased their refuge use from low to high predation risk (estimate \(\pm\) SE \(= 0.292 \pm 0.119\), \(F_{1,26} = 5.42\), \(P = 0.03\); Fig. 1a) and they significantly decreased their refuge use from foraging to mating treatments (estimate \(\pm SE = -0.290 \pm 0.118\), \(F_{2,26} = 4.75\), \(P = 0.04\); Fig. 1b). In the multidimensional model the interaction term between the main effects was statistically significant (estimate \(\pm SE = -0.539 \pm 0.136\), \(F_{2,24} = 15.01\), \(P < 0.0001\); Fig. 1c). Squirrels spent the least amount of time in the refuge in the mating/low predation risk combination, differentiating between the odour treatments at low predation risk, but not at high predation risk (Fig. 1c).

**Personality of Antipredator Behaviour**

Squirrels’ refuge use was repeatable across the combinations of manipulated environmental variables. The random intercept term representing the variance attributed to animal personality was significant in all three sets of models (LRT 1a–c versus 2a–c; Table 1). The random slope terms representing individual variance in plasticity were not significant in models that tested the slope of a factor in the absence of another factor (LRT 2a versus 3a, 2b versus 3b, 2c versus 3c, and 2c versus 4c; Table 1). However, the random slope terms were significant for the model including both factors (LRT 3c versus 5c and LRT 4c versus 5c; Table 1). This difference shows that when a second variable is affecting individual plasticity, inclusion of that second random slope can increase power to detect significance of the first random slope. Last, the interaction of the two random slope components was not significant (LRT 5c versus 6c; Table 1). In other words, squirrels had significant individual differences in their responsiveness to each environmental variable, but not significant individual differences in their responsiveness to...
particular combinations of those environmental variables. These results regarding random slope terms relate to consistent individual differences in plasticity that we address below.

**Consistent Individual Differences in Plasticity of Antipredator Behaviour across Secondary Environments**

Male *U. beldingi* showed consistent individual differences in plasticity when plasticity was measured in different environments. When considering the amount of plasticity shown across high and low predation risk, plasticity was significantly correlated between the foraging and mating environments (rs = 0.427, N = 27, p = 0.03; Fig. 2a). Likewise, when considering the amount of plasticity shown across mating and foraging environments, plasticity was significantly correlated between the predation risk manipulations (rs = 0.597, N = 27, p = 0.001; Fig. 2b). Because the difference scores factored out any among-individual variation due to the second variable, these results correspond to the tests of random slopes where the second variable is included to account for its variance (LRTs 3c versus 5c and 4c versus 5c; Table 1).

**DISCUSSION**

In nature, animals encounter variation in a range of environmental variables. Mating, foraging, high predation and low predation risk environments present different costs and benefits to Belding’s ground squirrels. When squirrels experienced different combinations of those variables, they showed significant multidimensional plasticity in refuge use, but also maintained consistent individual differences. The plastic response of squirrels’ refuge use to an environmental variable was also repeatable when measured at different levels of a second environmental variable. To date, researchers have described behavioural variation across change in a number of environmental variables in many species (reviewed in: Betini & Norris, 2012; Briffa, Bridger, & Biro, 2013; Carter, Goldizen, & Heinsohn, 2012; Dingemanse et al., 2010; Rodríguez-Prieto, Martin, & Fernández-Juricic, 2011). We know less about behavioural variation in response to change in combinations of environmental variables (but see Stahlschmidt & Adamo, 2013; Stahlschmidt & DeNardo, 2010; Westneat et al., 2011). Our results are consistent with previous reports of personality and plasticity, but indicate complex patterns of variation when behaviour is repeatedly expressed across combinations of multiple environmental variables.

Belding’s ground squirrels’ antipredator behaviour varied in response to the environmental manipulations. As expected, male *U. beldingi* showed more refuge use in a situation indicating high predation risk than in one indicating low predation risk (Fig. 1a). We predicted that male *U. beldingi* would use the refuge less in the mating environment than in the foraging environment due to the greater evolutionary payoff of a potential mate versus a potential meal. This prediction assumes that individuals are sufficiently fed and in good condition, which was the case with our laboratory rearing regime but may not be the case in nature. We also add caution to our functional interpretation of the effect of this factor because we compare refuge use between these two levels rather than comparing how each differs from a no-scent control. Still, the model comparing only the foraging environment to the mating environment supported our prediction (Fig. 1b). However, these two results obtained from traditional unidimensional approaches to phenotypic plasticity do not adequately describe the full range of variability attributed to the environmental manipulations. The multidimensional model showed a significant interaction effect of the environmental manipulations on antipredator behaviour (Fig. 1c). In other words, the effect of one environmental
manipulation depended on the level of the other. Male *U. beldingi* spent the least time inside the refuge in the mating/low predation combination. Squirrels showed greater differences in the proportion of time spent in the refuge between the mating and foraging environments in the low predation risk environment. They spent more time in the refuge in the high risk environment, but did not differentiate between foraging and mating environments when under high risk. The interaction effect may occur due to a balance between current and future reproductive efforts. Males have multiple mating opportunities within and across seasons, and so the lack of differences in the proportion of time using the refuge between mating and foraging treatments in the high predation risk environment may reflect a conservative tactic to ensure survival to future reproductive opportunities. Both environmental variables are relevant to explaining variation in antipredator behaviour of male *U. beldingi*. However, the interaction term overlooked by unidimensional models is also important, and a potentially adaptive facet of behavioural variation in this species. Multidimensional plasticity may be adaptive in other species, such as the interaction between brood size and nesting age on parental behaviour in house sparrows (Westneat et al., 2011). Also, in Children's pythons, *Antaresia childreni*, temperature and humidity have an interactive effect on parental behaviour (Stahlschmidt & DeNardo, 2010).

Together, these results demonstrate the benefit of addressing combinations of environmental variables and their effect on behaviour.

Despite the multidimensional plasticity shown by male *U. beldingi*, we still found consistent individual differences in squirrels’ refuge use across all combinations of environmental manipulations. The consistent individual differences in refuge use may be due to genetic polymorphisms arising from selective pressures, but an additional potential explanation is that personality reflects differences due to environments that the individuals previously experienced prior to our manipulations. Development influences animal personality (Duckworth, 2010; Sih, 2011; Sih et al., 2004; Simm, Gosling, & Moltschaniwskyj, 2008; Stamps & Groothuis, 2010), and our results point towards more complex effects of plasticity on personality. Stamps and Groothuis (2010) noted that the term behavioural plasticity is applied indiscriminately to when behaviour changes as a function of current environments or previously experienced environments. A plastic response can persist and the behavioural effect remains in the absence of, or change in, the environmental variable. Conversely, a plastic response may be ephemeral, and the effect on behaviour changes once the current environment changes. If an environment’s effect on behaviour is lasting, differences in the time of onset (Butler, Toomey, McGraw, &

---

**Table 1**

<table>
<thead>
<tr>
<th>Model</th>
<th>Fixed effects</th>
<th>Random intercept</th>
<th>Random slopes</th>
<th>Likelihood</th>
<th>Test</th>
<th>LRT</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unidimensional plasticity</td>
<td>1a Odour</td>
<td>—</td>
<td>—</td>
<td>−153.8</td>
<td>1a vs 2a</td>
<td>51.42</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2a Odour</td>
<td>ID</td>
<td>—</td>
<td>—</td>
<td>−127.4</td>
<td>2a vs 3a</td>
<td>0.98</td>
<td>2</td>
<td>0.614</td>
</tr>
<tr>
<td>3a Odour</td>
<td>ID Odour</td>
<td>—</td>
<td>—</td>
<td>−127.0</td>
<td>1a vs 2a</td>
<td>51.42</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Unidimensional plasticity</td>
<td>1b Pred</td>
<td>—</td>
<td>—</td>
<td>−153.8</td>
<td>1b vs 2b</td>
<td>50.70</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2b Pred</td>
<td>ID</td>
<td>—</td>
<td>—</td>
<td>−127.4</td>
<td>2b vs 3b</td>
<td>4.08</td>
<td>2</td>
<td>0.130</td>
</tr>
<tr>
<td>3b Pred</td>
<td>ID Pred</td>
<td>—</td>
<td>—</td>
<td>−125.4</td>
<td>1c vs 2c</td>
<td>52.82</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Multidimensional plasticity</td>
<td>1c Pred-Odour</td>
<td>—</td>
<td>—</td>
<td>−152.5</td>
<td>1c vs 2c</td>
<td>52.82</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2c Pred-Odour</td>
<td>ID</td>
<td>—</td>
<td>—</td>
<td>−121.3</td>
<td>2c vs 3c</td>
<td>3.30</td>
<td>2</td>
<td>0.19</td>
</tr>
<tr>
<td>3c Pred-Odour</td>
<td>ID Odour</td>
<td>—</td>
<td>—</td>
<td>−119.7</td>
<td>3c vs 4c</td>
<td>4.95</td>
<td>2</td>
<td>0.08</td>
</tr>
<tr>
<td>4c Pred-Odour</td>
<td>ID Pred</td>
<td>—</td>
<td>—</td>
<td>−118.9</td>
<td>4c vs 5c</td>
<td>13.29</td>
<td>3</td>
<td>0.004</td>
</tr>
<tr>
<td>5c Pred-Odour</td>
<td>ID Pred-Odour</td>
<td>—</td>
<td>—</td>
<td>−113.1</td>
<td>5c vs 6c</td>
<td>11.65</td>
<td>3</td>
<td>0.009</td>
</tr>
<tr>
<td>6c Pred-Odour</td>
<td>ID Pred-Odour</td>
<td>—</td>
<td>—</td>
<td>−109.3</td>
<td>5c vs 6c</td>
<td>7.60</td>
<td>4</td>
<td>0.13</td>
</tr>
</tbody>
</table>

Odour: categorical variable representing mating and foraging manipulations; Pred: categorical variable representing high and low predation risk manipulations; ID: squirrel identity; LRT: $\chi^2$ value for the log likelihood ratio test. Significant P values (<0.05) are shown in bold.

---

**Figure 2.** Consistent differences in individual plasticity across different environmental contexts. (a) The difference score (i.e. plasticity) between refuge use in the mating environment and the foraging environment was calculated in both high and low predation risk environments and the plot shows their correlation. (b) The difference score between refuge use in the high and low predation risk environment was calculated in both foraging and mating environments and the plot shows their correlation. Both correlations were significant ($P < 0.05$).
Belding multidimensional plasticity of antipredator behaviour in male predator behaviour was a consistent trait with the potential to be a b). This repeatability of plasticity will impact how selection oper-
ioural plasticity among individuals, in some cases showing differences in plasticity across other environmental variables. Although asking whether plasticity is repeatable may seem coun-
dividual differences in the slope interaction term, although that variable is repeatable across multiple levels of other environments. Consistent individual differences in behaviour, or animal personality, persisted across manipulations of combinations of environmental variables. Furthermore, squirrels showed consistent individual differences in plasticity when plasticity in response to one environmental variable was measured at different levels of a second environmental variable. Together, these results clarify patterns of behavioural variation in response to complex, realistic environmental variation animals encounter in nature. A number of traits other than behavioural traits respond to such environmental variation, and so these data should benefit a variety of fields in addition to animal personality, such as evolutionary physiology (Zera, Harshman, & Williams, 2007) and life-history theory (Nussey, Wilson, & Brommer, 2007).

Acknowledgments

We thank the American Museum of Natural History Theodore Roosevelt Memorial Grant, American Society of Mammalogists Grants-in-Aid, University of Chicago Hinds Fund and Valentine Eastern Sierra Reserve Grant for funding. Mateo lab members, Trevor Price, Liz Scordato and Jason Watters all provided helpful comments. Katie Brooks, Kevin Bender, Karen Fowler and Tamara Rocabado all helped with field work and Jack Phillips helped score videos.

References

Mateo, J. M., van den Hout, P. J., Piersma, T., Kempenaars, B., Réale, D., & Dingemanse, N. J. (2011). Disentangling the roles of frequency- vs. state-