Animal Behaviour 90 (2014) 109–116

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Andy Dosmann*, Jill M. Mateo [1]

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

ARTICLE INFO

Article history:
Received 4 September 2013
Initial acceptance 30 September 2013
Final acceptance 3 January 2014
Available online 26 February 2014
MS. number: A13-00725R2

Keywords:
animal personality
antipredator behaviour
behavioural plasticity
ground squirrel
multidimensional plasticity
Urocitellus beldingi

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.

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

* Correspondence and present address: A. Dosmann, Stanford University, Sweet Hall, 590 Escondido Mall, Stanford, CA 94305, U.S.A.
E-mail address: dosmann1@gmail.com (A. Dosmann).
[1] *E-mail address:* jmateo@uchicago.edu (J. M. Mateo).

0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2014.01.011

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 shyer. 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. In a sample of wild-caught, captive male *U. beldingi*, we 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 trapped males from Rock Creek Canyon, CA, housed them individually in plastic cages (38 × 33 × 11 cm; solid sides and bottom, wire lid) with pine bedding and dry grass, and provided them with five pieces of Mouse Diet 5015 (LabDiet, Richmond, IN, U.S.A.) and water ad libitum. We maintained a 13:11 h light:dark cycle to mimic the natural cycle, and maintained temperature using a heater at night and a combination of fans and/or an air conditioner during the day. In 2009, average daily temperature (±SD) at 1000 hours was 55.4 ± 2.6 °F (12.4 ± 1.4 °C). After 2009, we switched to a thermometer that recorded daily minimum and maximum temperatures, which averaged 56.7 ± 2.0 °F (13.7 ± 1.1 °C) and 72.7 ± 5.6 °F (22.6 ± 1.7 °C). We tested males over the course of a few weeks during the mating season, giving roughly 1 week for acclimation to captivity before testing and 1 week between test repetitions. Tests occurred before or within a few days of our last observed mating in the field. Males had descended and pigmented testes, which indicates sexual capability. We collected data between 2009 and 2011, testing 27 males across the manipulated environments, and an additional 11 males to control for potential order effects in the experimental design (see below). After testing, we released the squirrels at their site of capture. During trapping we took a number of measures to minimize stress. We checked traps every 10–15 min, but more regularly if weather conditions were less than ideal. After an individual was captured, we placed it in the sun or shade as appropriate for the temperature, and provided a small amount of peanut butter as food until transport to the animal quarters. Institutional Animal Care and Use Committees (IACUC) at University of Chicago (protocol no. 71255) and University of California at Santa Barbara (protocol no. 5-03-532) approved this study, which adhered to standards set forth by the ASAB/ABS Guidelines for the Use of Animals in Research and by the U.S. National Institutes of Health for animal research. We had permits from California Fish & Game and U.S. Forest Service.

Test of Refuge Use

We measured antipredator behaviour of *U. beldingi* in a refuge use test. We focused 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 (Briffa 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 a 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