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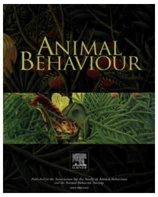

Differences in environmental enrichment generate contrasting behavioural syndromes in a basal spider lineage

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Behavioural syndrome studies are commonly descriptive and often find a relationship between boldness, shyness and exploration. However, the mechanisms underlying behavioural syndromes are not well understood. In the present study, we examined the extent to which early experience acts as a modifier of behavioural tendencies in the basal tarantula, *Brachypelma smithi*. Juvenile individuals were housed for 2 years either in enriched controlled conditions, or in restricted (minimal) conditions. Behavioural assays were completed both in short-term and in long-term increments. We found both short-term and long-term differences in multiple contexts of behaviour between treatments. In addition, individuals in the enriched treatment developed correlations between several behavioural traits whereas individuals in the restricted treatment did not. This result suggests that early environment can induce behavioural syndromes in some populations, or conversely, that continual stress may break down normal behavioural development and thus prevent a behavioural syndrome from emerging. This study provides a cautionary tale for those studying behavioural syndromes in captivity, and because this is a basal spider species, it provides important insight into the evolution of spider behavioural syndromes.

Behavioural syndromes, or correlated suites of behavioural traits across time, situations or ecological contexts, have been described nearly ubiquitously for animal populations (Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). Although there is species-specific variation in the traits included in these syndromes, most studies of behavioural syndromes involve variation in traits reflecting boldness, exploration or aggression, meaning that some individuals are consistently more bold, explorative or aggressive than other individuals.

These behavioural correlations can result in apparently nonadaptive behaviour (i.e. 'spillover'). For example, an individual with a bold behavioural type may be favoured to forage boldly in the absence of predators to increase resource acquisition, whereas showing the same behaviour in the presence of a predator increases its risk of becoming prey. Alternatively, an individual with a shy behavioural type may hide in both contexts, thus avoiding predation but also failing to exploit the resource (Riechert & Hedrick, 1993; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, et al., 2004). However, the presence of such trait correlations generally reflects adaptation either because (1) populations are exposed to different selective environments and thus exhibit behavioural ecotypic variation (Bell & Sih, 2007; Dingemanse et al., 2007; Riechert, 1999), or because (2) individual differences in behavioural type decreases potential competition among conspecifics (reviewed in Bolnick et al., 2003).

Most behavioural syndrome studies offer a description of the behavioural syndrome, or alternatively measure the result of interactions between individuals of different behavioural types (e.g. Pruitt, Riechert, & Jones, 2008; Sih & Watters, 2005). The underlying mechanisms maintaining correlations are not well understood. Pleiotropy or linkage disequilibrium is suggested from studies that have examined population crosses or obtained heritability estimates (Kralj-Fišer & Schneider, 2012; Pruitt & Riechert, 2009a, 2009b; Riechert & Hedrick, 1993; Riechert & Smith, 1989). Smith and Riechert (1984) first suggested that behaviour is correlated with hormone titres, something that Sanogo, Hankison, Band, Obregon, & Bell (2011) have revisited.

In the present study, we examined the extent to which early experience acts as a modifier of inherited behavioural tendencies. DiRienzo, Pruitt, and Hedrick (2012) provided evidence of this factor in the cricket *Gryllus integer*. On exposing males to high call volumes during development, they obtained reduced individual aggressiveness in these males in male–male agonistic disputes compared to males reared in silence.

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Here we test the extent to which a restrictive natal environment modifies an individual's behavioural type in the tarantula, *Brachypelma smithi* (Araneae, Theraphosidae). We reared individuals either under a more normal control environment, or under a restrictive condition. We then performed a series of behavioural assays developed to assess spider behavioural type, at short- and long-term intervals.

METHODS

Juvenile Environment

Forty-two third-instar (one moult removed from emergence from the eggcase) *B. smithi* were selected at random from 40 different pairs of parents, owned by a private breeder. All test subjects were reared in our laboratory between 19 and 23 °C in ambient light conditions. Each spiderling was offered three live crickets matched to its current size every 3–4 days. At each feeding session, we removed all debris present (i.e. shed moults and cricket remains). Each tarantula had drinking water available at all times via a glass watering tube and wick, and we misted the containers once a week during one of the feeding sessions.

All spiderlings were individually housed in rectangular, transparent plastic containers (10 × 15 × 10 cm) and were moved into 20 × 30 × 15 cm containers following the fourth instar. Twenty-one spiderlings chosen at random were assigned to the control environment. Each of these control spiderlings was provided sufficient substrate (mixture of sand and potting soil) to dig a burrow of 5–7 cm in depth. An artificial English ivy leaf offered cover. The control conditions mimicked those offered in nature. The remaining 21 spiderlings were assigned to a restrictive environmental treatment in which they received no substrate for digging a burrow and no vegetation for potential shelter.

Behavioural Assays

Following 12 months of rearing in the respective control and restrictive environments, we scored each individual's behavioural type in the following trials: boldness in response to a predatory cue, latency to attack prey, tolerance towards conspecifics and neophobia. Each trial described was repeated a second time after a lapse of 3 weeks. To avoid habituation to disturbance, we allowed at least 72 h to lapse between each test on a particular spider. All assays were conducted between 1200 and 2000 hours. The order of behavioural assays was arbitrarily assigned for each spider to control for order effects (Bell, 2013). The test subjects were then maintained in the same treatment for a second 12-month period and the set of trials repeated as described above. To facilitate transport between the home containers and the testing arena (where applicable), we used a wire prod to coax spiders into a plastic box.

Boldness in response to a predatory cue

We removed each spider from its home container and placed it in a small (22 cm diameter) circular track. After allowing the spider 5 min to acclimate to the track, we prodded the spider from a randomly assigned front or rear direction using a rubber-padded rod. Seventy-two hours later, we completed a second prod test on the opposite side of the spider as the previous test. We then recorded the distance that the spider travelled in response to each prod. Individuals that showed greater retreat distances in response to the prods were considered less bold than individuals that showed shorter retreat distances (Riechert & Johns, 2003).

Latency to attack prey

As hunger is expected to affect an individual's response to a prey item, we ran trials for latency to attack prey on a scheduled feeding day. At the initiation of a trial, we dropped a cricket approximately 1 cm in front of the spider in its home container. We recorded the time between the cricket being dropped and the spider's first attack (i.e. lunge at the prey) as the individual's latency to attack prey.

Conspecific tolerance

Although *B. smithi* is a solitary species, conspecific tolerance and aggression are important for fitness and survival during dispersal and mating in spiders. For example, individuals with lower tolerance for conspecifics are more likely to be injured or killed during antagonistic encounters (Riechert & Hedrick, 1990). To test whether this attribute varied between our rearing treatments, we randomly selected pairs of spiders from the same treatment and marked each spider on the top of the abdomen with a different colour of fluorescent powder to distinguish between them. The spiders were then placed in a novel arena measuring 16 × 16 × 5 cm. We surrounded the arena with an opaque screen to minimize both visual and air current stimulation. During a 1 h monitoring period, we recorded the total number of aggressive encounters as well as the aggressor and the retreating spider in each encounter.

Neophobia

The level of neophobia, or the fear of new environments, may affect exploratory, foraging and/or mate-seeking behaviour. This may ultimately limit more neophobic spiders to smaller ranges. For this trial, we placed each spider individually in a novel arena of 22 × 22 cm with a cotton cloth substrate (to ensure the arena was novel to both treatments) with a 1 × 1 cm grid pattern printed on it. Using the grid, we recorded the travel pattern of each spider, and thus, the distance travelled in the arena for 15 min.

Statistical Methods

All statistical computations were completed using Minitab 14 software (State College, PA, U.S.A.) and R version 2.15.1 (R Foundation for Statistical Computing, Vienna, Austria). We used an analysis of similarity (ANOSIM; Clarke, 1993) to compare the behavioural tendencies of both treatments across all four assays at the two time points, using an alpha value of 0.025. We applied Kruskal–Wallis tests (Theodorsson-Norheim, 1986) to compare the average trait values (e.g. mass, body length) across treatments and the Brown–Forsythe test (Algina, 1994) to compare variation in behaviour across treatments (e.g. latency to attack prey). We used a Bonferroni-corrected alpha value of 0.005 across assays to account for repeated measures of each spider. We performed Spearman rank correlations to assess whether individual differences in behaviour were repeatable across short- versus long-term intervals.

RESULTS

Four test spiders died during the process of moulting in the study ($N = 1$ control, $N = 3$ restricted). No data from these spiders were included in the analyses. No treatment differences were detected in spider body mass ($P = 0.44$) or body length ($P = 0.83$). Average mass was 8.24 g and average length was 3.1 cm. The combined behavioural tendencies of both treatments differed significantly at both time intervals (ANOSIM: year 1: $P < 0.0001$; year 2: $P < 0.0001$). Thus, when considering all four behavioural assays in a combined multivariate analysis, the treatments exhibited wildly divergent behavioural profiles.