ANIMAL BEHAVIOUR, 2008, **75**, 309–318
doi:10.1016/j.anbehav.2007.05.026

Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*

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*(Received 7 July 2006; initial acceptance 12 September 2006;
final acceptance 4 May 2007; published online 3 December 2007; MS. number: A10501R)*

An increasing number of studies are focusing on the role of animal temperament in the ecology of wild populations. One important step in these studies is to estimate the repeatability of temperament traits, by replicating measures of an animal's behavioural or physiological reactions to a novel or stressful situation. When studies are performed in the field, several factors can affect repeatability estimates: (1) microenvironmental conditions prior to or during a test may affect the measured behaviour, and spatial heterogeneity in predation risk within the habitat of a population may affect repeatability; (2) a decrease over time in the strength of behavioural reactions as a result of habituation may bias repeatability; and (3) individuals may differ in their habituation. In this study we used a linear mixed-model approach to test for the occurrence of interindividual variation in behavioural reaction and habituation of eastern chipmunks, *Tamias striatus*, to a hole-board test and a handling bag test. We found high intraindividual consistency for the behaviours recorded both in the hole-board and handling bag tests; four temperament traits could be considered (i.e. activity/exploration, reaction to stress, emotionality and docility). Given that we found no phenotypic variation in habituation, chipmunks seem to show a behavioural carryover in activity/exploration and docility, which could have consequences for the evolutionary potential of habituation to novelty.

Keywords: behavioural syndrome; docility; eastern chipmunks; exploration; habituation; hole-board; *Tamias striatus*; temperament trait

The evolutionary and ecological implications of temperament, personality, or coping style have recently experienced a growing interest (Wilson et al. 1994; Wilson 1998; Koolhass et al. 1999; Dingemanse et al. 2003; Réale & Festa-Bianchet 2003; Dall et al. 2004; Sih et al. 2004; Bell 2005; Carere et al. 2005). Temperament and personality are assumed to play an important role in many aspects of an animal's behavioural repertoire including habitat use, predation avoidance, dispersal, or social behaviour (Dingemanse et al. 2003; Dall et al. 2004; Sih et al. 2004; Dingemanse & Réale 2005). Furthermore, recent studies have shown that temperament traits can affect several components of fitness (Dingemanse & Réale 2005). The concept of temperament is defined as consistency of an individual's behavioural responses over time and/or across situations (Réale et al. 2007). To advance in the evolutionary ecology of temperament, it will be necessary to validate the methods by which we measure temperament traits in the field and to understand the components of the phenotypic variation observed in a natural population. Several factors may complicate the study of temperament in the field.

Field experiments often suffer from an inability to control environmental conditions during the test and this may affect our way of estimating an individual's behavioural consistency (i.e. the ranking of individuals across repeated trials). The behavioural response of an individual recorded in experiments used to measure temperament traits, such as open-field tests (Archer 1973), novel object, or startle tests, may therefore differ according to the environmental conditions during the test (Archer 1973; Mettke-Hoffmann et al. 2006; but see Eilam 2003). For example, light intensity or condition of transfer of animals prior to the test can affect behaviour in an open-field (Archer 1973; Walsh & Cummins 1976), and complex objects elicit more exploration than less

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0003–3472/08/$30.00/0

complex objects (Mettke-Hoffmann et al. 2006). An animal may therefore show different responses to a temperament test, only because of the specific microenvironmental conditions prior to or during the test (Henderson 1990). In the absence of information or control of some environmental conditions during a test, an experimenter may obtain spurious results about the rank of behaviour responses amongst different individuals (Fig. 1). In particular, environmental effects may mask consistent differences between individuals when the range of variation in the behaviour across situations is higher than the range of behaviour responses amongst individuals within each particular situation (Hayes & Jenkins 1997). This may be especially problematic for an open-field test performed in field conditions without any knowledge about how animals perceived the risks related to different areas of the habitat.

One way to circumvent this issue is to repeat the test at least twice for each individual and to estimate interindividual variation and behavioural individual consistency (Henderson 1990; Hayes & Jenkins 1997; Réale et al. 2000; Dingemanse et al. 2002). In the case of temperament, this method might still be associated with problems. Many tests of temperament consider novelty as the environmental component at the origin of the stress (Wilson et al. 1994). However, sensitization or habituation to novelty can occur with repeated tests (Groves & Thompson 1970; Archer 1973; van Oers et al. 2005). For example, exploration declines with the number of times the test is replicated, in open-field tests (Archer 1973; Dingemanse et al. 2002), startle tests (Glowa & Hansen 1994; van Oers et al. 2005), or novel object tests (Mettke-Hoffmann et al. 2006). After estimating consistency of a behavioural trait, one may want to obtain a single value per individual (i.e. behavioural profile) to use in subsequent analyses. The common approach used is to average the values of a trait over repeated tests. Because of habituation, sensitization, or an accumulation of stress with number of tests (Paz-Viveros et al. 1997) averaging the values of repeated tests may provide misleading values about the rank of behaviour responses amongst individuals, particularly when animals have been tested a different number of times. Furthermore, individuals may differ in the way they assess the risk associated with a novel situation (Augustsson & Meyerson 2004) and may differ, not only in their original response to novelty, but also in the speed with which they habituate. For example, experiments on humans have provided some supports to the expectation that extraverts habituate faster than introverts (LaRowe et al. 2006), and rat or mouse strains differ in their habituation to an acoustic startle test (Glowa & Hansen 1994) or to an open-field test (Bolivar et al. 2000). Similarly, differences in habituation can be found between individuals from the two sexes (Elliot & Grunberg 2005; van Oers et al. 2005). Classical methods to estimate repeatability do not consider interindividual variation in habituation, and this omission may underestimate behavioural consistency (Hayes & Jenkins 1997).

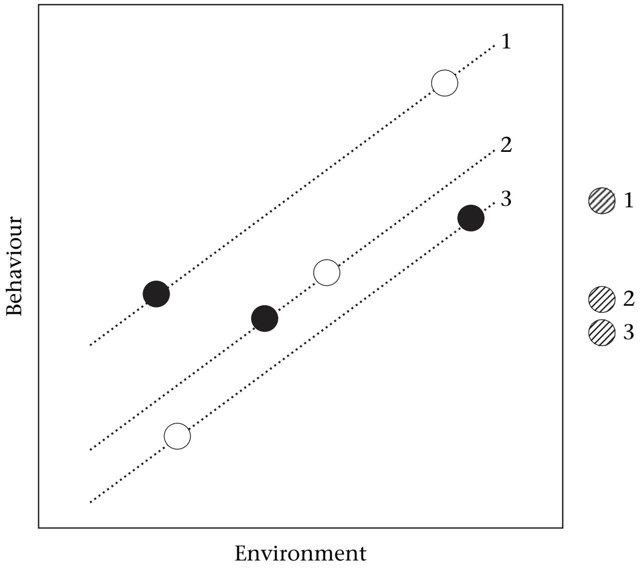

Figure 1. Individual behavioural responses (dotted lines) to environmental change for three hypothetical individuals. In the absence of information on a particular environmental condition during a test, an experimenter who collects only one record of the behaviour for each individual (closed circles) may obtain spurious results about the rank of behaviour responses amongst individuals. By averaging the data on replicated measurements of the behaviour on each individual (striped circles), the experimenter reduces the risk of assigning a wrong rank to individuals. Note that interindividual differences may be overestimated if replicated measures of the behaviour for each individual are highly correlated with environment (i.e. presence of individual–environment correlation).

Despite the potentially confounding effects of environmental variation and habituation on reaction to novel stimuli, few studies have considered the impact of environmental conditions on exploration in wild animals (Mettke-Hoffmann et al. 2006), and to our knowledge none have investigated interindividual variation in habituation in animals or its effect on the measurement of temperament or personality traits. The absence of interindividual variation in habituation would indicate a behavioural carryover (Sih et al. 2004) in the trait under study (e.g. exploration, activity, stasis, ...). Whether a behavioural trait shows carryover could therefore be important to our understanding of how animals cope with habitat heterogeneity, predation risk, or human disturbance. The existence of a behavioural carryover in a behavioural trait across repeated situations (i.e. no individual variation in rate of habituation) would also have important consequences for our understanding of the behavioural ecology of habituation; the absence of individual phenotypic variation in the rate of habituation would potentially imply an absence of genetic variation for the trait, which would constrain the potential evolution of habituation even in situations favouring it. In the case of discrete environmental situations, people generally use a character state approach (i.e. correlation between the two environmental situations) to illustrate a behavioural carryover (Sih et al. 2004). In the case of continuous environmental variation (i.e. decreasing novelty; population density...), however, such an approach is not the most appropriate and can be replaced by the reaction norm approach (Nussey et al. 2007). In these conditions, the presence of a behavioural carryover can be tested by comparing