REVIEW

The importance of wild populations in studies of animal temperament

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Abstract

Animal temperament describes behavioural differences between individuals that are consistent across time and contexts. Variation in animal temperament is rapidly gaining interest and attention within behavioural and evolutionary ecology. If we are to understand the causes and consequences of temperament variation within and between populations we need to determine the selection pressures that affect temperament in natural environments. To date, however, the vast majority of temperament studies have been carried out on captive-bred individuals. This review highlights potential problems that arise from using captive animals to elucidate the ecological and evolutionary functions of temperament in wild populations. For example, development, learning and environmental variability can all affect behaviour. Thus, both environment and gene-by environment interactions can affect the fitness functions of different temperaments, and hence selection. We stress the need for measurements of repeatability and heritability, and the importance of biological and ecological validation of temperament tests in wild animals. We describe the limited evidence from wild populations of the fitness consequences of temperament variation, and the use of intra- and inter-specific comparisons to prove adaptation. To identify multiple axes of behavioural variation, and how these interact with environments that vary spatially and temporally, we need long-term studies on wild populations – yet few studies of this nature currently exist. Finally, and perhaps counter-intuitively, we suggest that there is much to be gained from incorporating some of the approaches and statistics employed in the much longer established field of human personality.

Consistent differences in behaviour between individuals, known as temperament (or personality), have long been studied by psychologists, using both humans and other animals as subjects (Gosling, 2001; Brosnan, Newton-Fisher & van Vugt, 2009). Research on non-humans has typically occurred in the laboratory, using rodent models to extend knowledge of human temperament and its effects on well-being and health. For example, there are many studies that have addressed addiction (Olmstead, 2006) and anxiety (Pawlak, Ho & Schwarting, 2008). Efforts to improve the production and welfare of domesticated animals have also had an interest in individual differences (Price, 1999). Recently there has been a surge in interest in the effects that temperament has in studies of behavioural ecology. While the existence of individual differences has long been recognized – for example, Krebs & Davies (1987) discussed different behavioural strategies such as 'producers' or 'scroungers' or individuals that respond differently to risk – the impact that such differences have on behaviour has only recently become

of interest for behavioural and evolutionary ecologists. Two main reasons for this have been the lack of consistent terminology (e.g. 'personality', 'temperament', 'coping styles' and 'behavioural syndrome' are all found in the literature), and the lack of an ecological and evolutionary framework for temperament studies (Wilson *et al.*, 1994; Gosling, 2001; Sih, Bell & Johnson, 2004*a*,*b*; Réale *et al.*, 2007).

Now, as has been highlighted in recent reviews, there is increasing awareness that individuals within a population are not always ecologically equivalent (Magurran, 1993; Bolnick *et al.*, 2003), and the fact that temperament affects fitness and selection has been widely recognized (Wilson, 1998; Dall, Houston & McNamara, 2004; Dingemanse & Réale, 2005; Réale *et al.*, 2007; Smith & Blumstein, 2008). These reviews have emphasized the potential evolutionary causes and functions of temperament (e.g. Dall *et al.*, 2004; Sih *et al.*, 2004*a*,*b*; Smith & Blumstein, 2008), and have linked temperament studies to other areas of interest to behavioural ecologists, such as behavioural genetics (e.g.

van Oers *et al.*, 2005), conservation biology (e.g. McDougall *et al.*, 2006; Réale *et al.*, 2007; Smith & Blumstein, 2008) and behavioural plasticity (e.g. Réale *et al.*, 2007; Dingemanse *et al.*, 2010). Studies of temperament in wild populations are noted in some of these reviews (e.g. Sih *et al.*, 2004a; Réale *et al.*, 2007). However, none have fully discussed the important role that field studies with natural populations play (but, see Dingemanse & Réale (2005) for discussion of the fitness consequences of temperament variation in wild populations).

It is well established that individuals within wild populations may show distinct and non-changeable alternative behavioural strategies, which are adaptive and confer different fitness benefits (Magurran, 1993; Gross, 1996; Smith & Skúlason, 1996). In contrast, non-categorical inter-individual variation in behaviour was traditionally seen as noise around averages (Wilson, 1998; Dall *et al.*, 2004), and not itself functional in terms of fitness. Individual variation is, however, a consequence of natural selection (Wilson, 1998; Dingemanse & Réale, 2005; van Oers *et al.*, 2005). Lack of recognition of this fact has led to neglect in the behavioural literature in terms of how and why individuals differ in their behaviour (Wilson, 1998; Dall *et al.*, 2004; Sih *et al.*, 2004a), that is, the fitness functions and evolutionary consequences of the individual variation.

Compared with the large number of studies on captive, usually captive-bred, populations, temperament has only rarely been studied in the wild. If the ecological and evolutionary function of temperament is to be elucidated, we need information on the selection pressures that affect temperament in natural environments (Dingemanse & Réale, 2005; Smith & Blumstein, 2008). There may also be important gene by environment interactions that help to shape temperament in natural populations (Merilä & Sheldon, 1999; Nussey, Wilson & Brommer, 2007; Dingemanse *et al.*, 2009) that studies of captive individuals will never reveal. Furthermore, knowledge of how ecological pressures act on temperament in wild populations may aid the maintenance and health of captive populations, for example in aquaculture (Huntingford *et al.*, 2006) and conservation (McDougall *et al.*, 2006). Emphasizing the importance of temperament studies on wild, preferably non-captive, animals is the aim of this review.

Problems of using captive animals to study temperament

Studies of temperament using captive animals are valid, and provide essential information, particularly about the genetic control of temperament. Knowledge of the causes and effects of temperament in animals that are maintained by necessity in captivity may improve their welfare. It also improves production in agriculture and aquaculture (Price, 1999; Huntingford, 2004), and increases the likelihood of breeding and reintroduction success in animals housed for conservation (McDougall *et al.*, 2006). There are, nonetheless, numerous limitations that may need to be taken into account when studying temperament in captive populations, many of which are avoidable by studying wild populations. Below we highlight seven kinds of possible limitation,

starting with those that relate to animals brought into captivity from the wild, and then considering those that have been bred in captivity:

Collecting and trapping animals to test

There is increasing evidence that selective trapping may occur when animals are captured (Biro & Dingemanse, 2009). This is because animals that are bolder, more explorative or simply more active, may encounter and enter traps more often. Indeed, 'trappability' of wild animals has been used as a measure of boldness in temperament studies (e.g. in bighorn sheep *Ovis canadensis*, Réale *et al.*, 2000; North American red squirrels *Tamiasciurus hudsonicus*, Boon, Réale & Boutin, 2008; collared flycatchers *Ficedula allbicolis*, Garamszegi, Eens & Janos, 2009). Trapping methods may also vary in their temperament-based selectivity (e.g. in pumpkinseed fish *Lepomis gibbosus*, Wilson *et al.*, 1993), so careful choice of method, or use of more than one method at a time, may mitigate this problem. Other evidence comes from fisheries research, where it has become clear that fishing-induced selection can be a product of temperament as well as size (Biro & Post, 2008; Uusi-Heikkila *et al.*, 2008). Selective trapping will result in captive populations that represent only a subset of phenotypes and genotypes from wild populations. Studying temperament, and its links with fitness, in these populations may lead to misleading results, which are not applicable to behaviour and selection in the wild. Furthermore, as indicated by the fisheries example, wild populations that are over-sampled may also incur changes in temperament.

Stress associated with capture, handling and captivity

Capture and transport of wild animals is associated with acute stress (Teixeira *et al.*, 2007; e.g. loggerhead sea turtles *Caretta caretta*, Gregory *et al.*, 1996; reindeer *Rangifer tarandus platyrhynchus*, Omsjoe *et al.*, 2009), but may also cause chronic stress (Dickens, Earle & Romero, 2009). Stress effects on behaviour may compromise temperament studies. Moreover, acute stress can affect individuals differently (e.g. in black rhinoceros *Diceros bicornis*, Kock *et al.*, 1990) in ways that can be linked to temperament. For example, in great tits *Parus major*, shy individuals had higher body temperature and breathing rate than bold individuals after handling by experimenters (Carere & van Oers, 2004). It is therefore frequently assumed that wild animals brought into captivity should be settled for a period of time, so that they can recover from this stress, and habituate to new conditions before behavioural observations commence. However, the length of time needed for habituation when animals are brought from the wild into captivity varies between species and has rarely been studied directly (e.g. in greenfinches *Carduelis chloris*, Ekman & Hake, 1990). Some studies (e.g. in brushtail possums *Trichosurus vulpecula*, Day & O'Connor, 2000) show that habituation to captivity is vital before use in behavioural experiments. In contrast, the likelihood of chaffinches *Fringilla coelebs* foraging naturally decreased with time in captivity (Butler *et al.*,

2006), suggesting that an habituation period is not always beneficial to temperament studies. Some animals may simply not show individual differences in captivity, even though they do in the wild (e.g. pumpkinseed fish, Wilson *et al.*, 1993).

Nevertheless, some researchers have successfully combined wild and laboratory studies in the same individuals. Wild animals can be brought into the laboratory for controlled behaviour trials, and potentially to provide samples and be individually marked, and subsequently released back into the wild and monitored. If individual behaviour in captivity is related to an ecologically valid behaviour or measure of fitness in the wild (e.g. exploration in the lab is correlated with dispersal in the wild in great tits, Dingemanse *et al.*, 2003; and habitat use in North American red squirrels, Boon *et al.*, 2008), then not only is the temperament assay a good predictor of wild behaviour, but the variable effects of stress can be either minimized or incorporated into the known temperament variation in that species.

Chronic stress, as demonstrated by suppression of immune function, reduced growth and reproductive dysfunction, is often associated with captive housing. It too can affect individuals in different ways. Studies of zoo animals demonstrate that chronic stress results in reduced reproductive success (e.g. in the houbara bustard *Chlamydotis undulata*, van Heezik & Seddon, 2001; and cheetahs *Acinoayx jubatus*, Terio, Marker & Munson, 2004), and that temperament can affect which animals breed successfully in captivity (e.g. more fearful cheetahs are less likely to breed in zoos; Wielebnowski, 1999).

Homogeneity of the captive environment

Natural environments can vary predictably, but also do so stochastically. In comparison, captive environments are inherently stable. However, animals vary in their ability to cope with change, and this is an important part of their temperament. Coping styles demonstrate co-variation in behaviour and physiology, and are somewhat synonymous with temperaments, in particular with the idea of correlated suites of behaviours across contexts, or behavioural syndromes (Sih *et al.*, 2004a,b). Coping styles, however, are seen in the literature as a dichotomy rather than as a continuum: Proactive individuals are defined as more aggressive and risk-taking, whereas reactive individuals are less aggressive, and take fewer risks, but also are more behaviourally flexible (Koolhaas *et al.*, 1999). Behavioural flexibility allows animals to adapt to changes and challenges in their environment, and is a form of phenotypic plasticity, distinct from the formation of adult phenotype via the interaction of genotype and environment during development. It is presumed to be costly, and to be itself under selection (Wilson *et al.*, 1994; Koolhaas *et al.*, 1999). This further implies that large gene by environment interactions are possible in the formation of temperament.

Implicit in this discussion is that temperament traits may have greater fitness in certain environments, or when environments are changeable either spatially or temporally (Wilson *et al.*, 1994; Wilson, 1998; Dingemanse *et al.*, 2004).

That is, as a result of their temperament, individuals may vary in their adaptation to different environments, and their ability to cope with environmental change. For example, great tit survival was related to temperament, and to environmental variation, which caused changes in competition for space and food. The effect was opposite for males and females, and reversed between years. Offspring survival was also related to parental temperament (Dingemanse *et al.*, 2004). In the North American red squirrel, female behaviour affected offspring growth and survival, but the direction of effects changed among years, suggesting an association between temperament, fitness and food supply (Boon, Réale & Boutin, 2007). In the lizard *Lacerta vivipara*, fitness varied with temperament between semi-natural populations housed at different densities. At low densities 'asocial' lizards survived better, but under these conditions 'social' females had better reproductive success (Cote, Dreiss & Clobert, 2008). These examples illustrate the importance of investigating spatial and temporal environmental variability when studying temperament in wild species. Indeed, it suggests that the outcome of temperament studies on populations held under unnaturally stable conditions could provide misleading results about the long-term fitness consequences of individual temperaments and their importance for selection.

Effects of relaxed natural selection in the captive environment

In captivity there may be both relaxation of natural selection, and the imposition of artificial selection. Captive animals live in very different environments compared with those they originate from. Even if captive conditions are designed to mimic those in the wild, animals will still be released from predation pressure, and be much more frequently disturbed by humans. They will be treated for diseases and so rely less on their own immune system, they will need less time to forage as food will be provided, and potentially they may be housed in very unnatural social situations (Price, 1999; Huntingford, 2004). Relaxation of natural selection could result in the persistence of behavioural traits and genotypes that would be selected against in the wild. This effect may be increased by inbreeding due to small founder population size and the accumulation deleterious mutations (Woodworth *et al.*, 2002).

Intentional artificial selection in the form of domestication generally results in less active and less aggressive animals that are easier to catch and handle (Kohane & Parsons, 1988; Price, 1999; Huntingford, 2004; McDougall *et al.*, 2006). The effects of unintentional artificial selection are insidious and just as important. For example, boldness may increase in captive populations that no longer experience predation (e.g. in oldfield mice *Peromyscus polionotus*, McPhee, 2004; and in brown trout *Salmo trutta*, Sundstrom *et al.*, 2004). Aggression may increase or decrease, depending on factors such as housing density and food supply: high density housing combined with localized and predictable feeding can result in selection for aggression in salmonids, via increased competition (Huntingford, 2004).

Unintentional artificial selection is likely to be omnipresent in captive populations, and involve all aspects of the captive environment. It can cause changes in life history, morphological and physiological traits, which may be linked to temperament traits (Huntingford, 2004; McDougall et al., 2006). It may also disrupt the functional links between temperament traits and as well as those between behavioural and other traits (Sih et al., 2004b; Réale et al., 2007), leading to selective changes to the correlations under study. This is obviously a problem in itself, but can also lead to non-adaptive trait combinations. For example, when coonstripe shrimp Pandala danae, were bred for 10 generations in the lab there was inter-individual variation in struggling during repeated handling. The resulting differential mortality rates led to unintentional selection for tamer individuals. It also led to loss of pigmentation, and an increased growth rate in individuals sampled in the 10th generation as compared with the founder population (Marliave, Gergits & Aota, 1993). It is unknown what fitness cost these changes would have in a wild population, either individually or in combination. Our point here is that it is not possible to fully investigate the fitness consequences and ecological roles of temperament in populations that no longer have the same range and distribution of temperaments as their wild counterparts.

Constraints on mate selection

There may also be constraints on sexual selection that affect temperament in captivity. The pool of potential mates is usually reduced, limiting both competition for mates and mate choice. Furthermore, temperament can be linked to fitness via sexually selected mechanisms, but these links may be disrupted in captivity. For example, in the guppy Poecilia reticulata, females prefer more colourful males (Endler, 1995). These males are also bolder, and more likely to escape predation attempts, thus suggesting an indirect fitness benefit to females via increased offspring viability (Godin & Dugatkin, 1996). In the collared flycatcher Ficedula albicollis, male risk taking during singing to attract a mate was correlated with exploration and risk taking in other contexts, and risk taking males got mates more quickly (Garamszegi, Eens & Toeroek, 2008). Consequently, not having a large pool of potential mates could shift or alter the temperament of offspring reared in captivity.

Non-genetic effects

Loss of a natural development can result in a different range of adult phenotypes in the absence of genetic change. Differences in temperament traits such as boldness and aggression can be caused by rearing environment, that is with no genetic change (e.g. in the endangered fish Skiffia multipunctata, Kelley, Magurran & Macías-Garcia, 2005; in cod Gadus morhua, Braithwaite & Salvanes, 2005 and in three-spined sticklebacks Gasterosteus aculuatus, Bell & Sih, 2007; Dingemanse et al., 2009). These problems are often closely monitored in captive populations being bred for conservation via breeding programs, particularly if animals

are to be released back into the wild (McDougall et al., 2006), but such close scrutiny is less common in the laboratory. It is difficult to carry out studies of temperament from an ecological view point without knowing the range of environmental factors that exist in the natural habitat. Maternal and developmental effects, environmental effects, experience and learning can all affect behaviour (Falconer & Mackay, 1996), and genetic by environment interactions can influence phenotype formation (Merilä & Sheldon, 1999; Dingemanse et al., 2009). Thus, even if studies are carried out on wild-caught individuals, fundamental knowledge of their ecology is essential.

Variability in coping with captivity

Finally, certain species may be more amenable to life in captivity than others. For example, species with very large ranges, or exclusive territories, may not survive within the confines of the laboratory. Species also vary in their amenability to handling and their potential to become tame (Price, 1999). As with other types of study using captive animals, there appears to be a bias in the temperament literature towards animals that are easy to house, with short life cycles, such as rodents.

Problems with wild animal temperament studies

Problems arising from wild temperament studies are primarily methodological. Given the paucity of studies of temperament on wild animals, it is difficult to cite literature that demonstrate these problems, but they are easy enough to imagine, as we describe in the following examples.

Logistical constraints

As is inherent with almost all field studies, there are increased logistical constraints involved in finding individuals and monitoring their behaviour. Mechanistic approaches that attempt to integrate studies of behaviour with physiological measures such as endocrine status are even more problematic, due to the difficulty of getting samples (without disturbing behaviour). Similarly, genetics studies are harder to carry out. For these reasons, the time required for field studies is generally considerably longer than that for laboratory studies with equivalent sample sizes. Furthermore, the increased variation caused by environmental, developmental and social variability in wild populations may mean that larger sample sizes are needed in order to detect significant effects and relationships. The irony exists that the complexity and variability inherent in natural situations, which is of primary interest in studies of temperament in wild animals, may render some studies of wild populations logistically untenable.

Observer effects

There is also an increased possibility of observer effects, because animals may not be habituated to human presence as needed for observations. In addition, some shy or fearful

individuals may simply never be seen or trapped by observers (e.g. in pumpkinseed fish, Wilson *et al.*, 1993), instantly biasing samples towards bolder individuals (Biro & Dingemanse, 2009).

Being able to track and recognize focal animals

It can be hard to individually identify animals in the wild. There are a variety of ways of marking wild animals (e.g. ringing in birds, visible implanted elastomer tagging in fish), and some techniques (e.g. passive integrated transponders and data loggers) can automatically record location and physiological data. Nevertheless, capturing, handling and marking individuals can be time consuming, and often induces a stress response in the animals. The size of such responses can vary between individuals, in ways that may be useful in predicting temperament (e.g. in great tits, Carere & van Oers, 2004; Fucikova *et al.*, 2009). These stressors, may also affect subsequent behaviour and body condition (e.g. in great tits, MacLeod & Gosler, 2006), and how long it takes an animal to recover is often unknown (Teixeira *et al.*, 2007). Studying animals that cannot be individually identified increases the probability of sample size inflation by unknowingly measuring the same individual more than once. It also means that necessary repeated measures, for example for quantification of repeatability and heritability, and long-term studies, for example of fitness outcomes, are impossible. Studies of the fitness effects of varying temperament are rare in wild populations (Smith & Blumstein, 2008), but vital to demonstrate the importance of individual behavioural variation on evolutionary processes.

Anthropogenic disturbance

Many animal populations are impacted at some level by human activities. There is an assumption that temperament measures in wild animals will represent traits that are adapted to the natural environment. However, if humans have manipulated the environment, then selection pressures may be altered. This can result in animals being maladapted to the environment they find themselves in, and ultimately to human-induced selection. The underlying concern here is that of 'contemporary evolution' (Hendry & Kinnison, 1999) where significant changes in traits such as temperament may occur in a few generations when selection pressures are sufficiently great (Endler, 1986).

An obvious example of this problem is when animals live close to humans. They may be disturbed by, or become habituated to, human activities (e.g. in ungulates, Stankowich, 2008), and may come to rely on the extra food they provide (Orams, 2002). These impacts may vary between individuals with temperament (e.g. in Eastern chipmunks *Tamias striatus*, Martin & Réale, 2008; yellow-eyed penguins *Megadyptes antipodes*, Ellenberg, Mattern & Seddon, 2009), suggesting selection for specific temperaments. Another key example is that of harvesting bias. Passive trapping methods selectively capture bolder individuals (Wilson *et al.*, 1993;

Biro & Post, 2008; Uusi-Heikkila *et al.*, 2008; see discussion above). Active methods such as hunting may also selectively remove animals with specific temperaments, because they may be encountered more frequently, and because hunters favour certain types of individuals. In addition, the removal of predators from ecosystems may cause indirect effects on the temperament of prey species (Berger, Swenson & Persson, 2001). These examples highlight the fact that temperament studies may provide useful information on how animals can adapt, via both phenotypic plasticity and genetic adaptation, to environmental changes caused by humans.

The current conceptual framework

How does temperament in wild animals fit within the current framework for temperament studies? There exist two main approaches to temperament studies in non-humans, and there has been an increase in theoretical discussion and reviews of these approaches (e.g. Wilson *et al.*, 1994; Wilson, 1998; Gosling & John, 1999; Gosling, 2001; Sih *et al.*, 2004*a,b*; Bell, 2007). Both emphasize that variation in specific behaviours contributes to composite traits that may then affect fitness (Réale *et al.*, 2007). One approach suggests that context-specific temperament traits have evolved under selection from different selection pressures that are themselves context specific. These traits may be only weakly correlated between contexts (Wilson *et al.*, 1994; Wilson, 1998). The second suggests groups of related behavioural traits, called syndromes, which are correlated either within a context, or across different contexts (Sih *et al.*, 2004*a,b*). Both approaches describe underlying genetic variation that affect physiological and behavioural outcomes, but the ideas underpinning behavioural syndromes also suggest that strong links exist between traits, based on neurological and hormonal mechanisms that affect suites of behaviours (Ketterson & Nolan, 1999). These links may create trade-offs across contexts that have important evolutionary consequences (Sih *et al.*, 2004*b*).

Currently, there is no clear consensus in the literature regarding these approaches, and it will likely transpire that both are valid; that is, that they represent different ends of a spectrum of explanations for consistent behavioural variation. A key aspect that now needs attention is to determine how temperament can be better integrated into ecology and evolution. Réale *et al.* (2007) have proposed a four-step process as part of a framework that addresses this. Briefly, these are: (1) Developing relevant experimental tests to measure temperament traits, including demonstration that there is measurable variation between individuals within a population, and that the traits measured are both repeatable and heritable. (2) Validating tests via phenotypic and genetic correlations between behavioural, physiological and ecological traits, and experimental manipulations of these relationships. (3) Linking temperament traits to fitness consequences. (4) Using intra- and inter-species comparisons to elucidate broad-scale relationships between ecological conditions and temperament. All of these steps can be investigated in wild populations, and doing so provides

important information on how temperament is linked to ecological and evolutionary processes. Below we explore each of these steps in more detail.

Variation, repeatability and heritability

Implicit in studies of temperament is the presence of measurable, consistent behavioural variation between individuals (van Oers *et al.*, 2005). Unfortunately, the repeatability of temperament variation is often not explicitly tested, particularly in the field, where repeated sampling of the same individuals may be very difficult (Bell, Hankison & Laskowski, 2009). Repeatability describes the proportion of phenotypic variance explained among individuals (Falconer & Mackay, 1996), and hence does not separate genetic and environmental variance in temperament, although it does set an upper limit to heritability (Boake, 1989).

Stirling, Réale & Roff (2002) state that published studies of temperament traits usually show significant heritability, with an average of 0.31, a figure which is comparable to those measured for life-history traits, but less than that for morphological traits. Most studies that have quantified the heritability of temperament measures in wild animals have used wild-caught parents and their captive-raised offspring (e.g. in great tits, Drent, van Oers & van Noordwijk, 2003; dumpling squid *Euprymna tasmanica*, Sinn, Apiolaza & Moltschaniwskyj, 2006; the poeciliid fish *Brachyrhaphis episcopi*, Brown, Burgess & Braithwaite, 2007). However, a few studies have used pedigree information of known individuals to calculate temperament heritability between wild parents and their wild offspring (great tits brought temporarily into the laboratory to measure exploration, Dingemanse *et al.*, 2002; Quinn *et al.*, 2009; and bighorn sheep tested in the wild, Réale *et al.*, 2009).

The vast majority of temperament studies to date have been lab based and most clearly try to exclude or minimize non-genetic sources of variation. The main exceptions to this are lab studies where animal models are used to investigate non-genetic effects on human conditions. For example, the effect of prenatal stress on future behavioural tendencies is a prolific area for study that relies largely on rodent models (Weinstock, 2008). In contrast, studies on wild animals need to identify both genetic and non-genetic sources of variation in temperament (e.g. in great tits, Quinn *et al.*, 2009), as well as interactions between these sources (see Nussey *et al.*, 2007, for details of different variance components and how they may interact). Non-genetic effects and gene by environment interactions do not preclude high repeatabilities if this variation causes a larger increase in behavioural variation between rather than within individuals (Lessells & Boag, 1987). For example, permanent environmental effects may cause repeatability whereas non-permanent effects may increase or decrease repeatability, depending on whether individuals remain in constant conditions either spatially or temporally (Nussey *et al.*, 2007). In a meta-analysis of repeatability studies, Bell *et al.* (2009) found that repeatabilities were actually higher in the field than in the laboratory. Thus, there may be adaptive advantages to behavioural consistency in the

wild (Dall *et al.*, 2004), or conditions in the wild may themselves create repeatability (Dingemanse *et al.*, 2010), or both. Either way, it highlights the need to study temperament in natural systems where non-genetic factors that affect temperament, and hence fitness, can be quantified within their ecological contexts.

Validating temperament tests

Determining the validity of temperament tests requires evidence that measurable behavioural variation is related to variation in physiological (biological validation) or ecologically important (ecological validation) traits (Réale *et al.*, 2007). Biological validation therefore requires evidence of variation in the neurological and/or endocrinological mechanisms that underlie behaviour (Sih *et al.*, 2004*b*). This may be difficult in the field, although new techniques such as remote sampling for hormone assays (Millspaugh & Washburn, 2004; Keay *et al.*, 2006) facilitate it. It is also possible to manipulate hormone levels in some wild populations, allowing experimental tests of the effects of physiology on temperament. This can be done for both adults (e.g. testosterone implants in red grouse *Lagopus lagopus scoticus*, Seivwright *et al.*, 2005; and white-footed mice *Peromyscus leucopus*, Grear, Perkins & Hudson, 2009) and offspring (e.g. corticosterone-injected eggs in yellow-legged gulls *Larus michahellis*, Rubolini *et al.*, 2005; and the lizard *L. vivipara*, Uller & Olsson, 2006).

Ecological validation is easier than biological validation in studies using animals in the wild. Indeed, a primary aim of field studies is to observe and manipulate animals within the ecological context to which they are adapted. It also provides a clear way to integrate studies of temperament into ecology. For example, temperament variation has been shown to affect natural dispersal in a number of taxa, with bolder individuals being more likely to disperse (e.g. killifish *Rivulus hartii*, Fraser *et al.*, 2001; great tits, Dingemanse *et al.*, 2003; lizards *L. vivipara*, Cote & Clobert, 2007).

Fitness consequences

There have only been a few studies attempting to determine fitness consequences of variation in animal temperament. These studies have primarily investigated the effect of variation in boldness (e.g. in pumpkinseed fish, Wilson *et al.*, 1993; and bighorn sheep, Réale *et al.*, 2000), exploration (e.g. in Merino sheep *Ovis aries*, Murphy *et al.*, 1994; and great tits, Dingemanse *et al.*, 2004) and aggression (e.g. in yellow-bellied marmot *Marmota flaviventris*, Armitage, 1986; and water striders *Gerris remigis*, Blanckenhorn, 1991) on reproductive success and survival. A recent meta-analysis by Smith & Blumstein (2008) used data from 31 studies on 25 species from a wide range of taxa, and found that bolder individuals had increased reproductive success, but at the cost of decreased survival. This suggests a fitness trade-off between contexts (Sih *et al.*, 2004*a*,*b*). In the meta-analysis, exploration also had a positive effect on survival, while aggression had a positive effect on reproductive success.

Smith & Blumstein (2008) state that 19 of these studies were carried out on wild animals. When using just these studies, they only found significant effects of boldness on survival, but obviously cannot rule out the effects of limited sample size. However, only five studies on four species actually involved wild animals in their natural habitats, so our knowledge of the ultimate consequences of temperament variation in natural populations is even more limited than the meta-analysis suggests.

Intra- and inter-species comparisons

Comparative approaches are important because proving that a temperament trait affects fitness does not prove that temperament is itself adaptive (Réale et al., 2007). Population and species comparisons allow past selective forces to be studied. They also provide another clear link between temperament and ecology (Uher, 2008), particularly if carried out on wild animals. Furthermore, they may allow the testing of hypotheses that would be difficult logistically or ethically to perform experimentally.

Intra-species comparisons provide a classic approach to the study of adaptation in the wild. In particular, they have been used to determine the effects of differences in predation regime and habitat on the life history, morphology and behaviour of fishes (e.g. guppies, Endler, 1995; and three-spined sticklebacks, Huntingford, Wright & Tierney, 1994). Inter-population comparisons of fish have now repeatedly highlighted the importance of environmental factors in shaping animal temperament (in *B. episcopi*, Brown, Jones & Braithwaite, 2005; and three-spined sticklebacks, Brydges et al., 2008; Dingemanse et al., 2009). Indeed, one strength of the comparative approach is that differences in temperament between populations (or species) are placed directly into an ecological context.

For these types of study to be robust, replication is vital, that is that multiple populations are tested from each environmental condition. In addition, even in well-studied systems, there are limits to the usefulness of such comparisons, because they cannot determine the relative importance of genetic and environmental effects. To do so requires raising offspring from different populations in novel and constant conditions to control for environmental effects (the 'common garden' approach, for example in nine-spined sticklebacks *Pungitius pungitius*, Herczeg, Gonda & Merilä, 2009), or carrying out reciprocal translocations of individuals with known temperament and then monitoring subsequent changes in fitness (Hereford, 2009; e.g. in the desert spider *Agelenopsis aperta*, Riechert & Hall, 2000).

Inter-species comparisons provide a similar approach in testing adaptive hypotheses, but have rarely been used in temperament studies. In a review of temperament in non-human primates, Clarke & Boinski (1995) show that temperament varies between species and between populations within species, and that these differences can be correlated with differences in social structure, foraging niche, territoriality and stress reactivity. However, it is important to note that to enhance validity, there is a need to control for

phylogenetic effects, and to avoid 'just so' explanations. This can be achieved via a priori hypotheses, with clear predictions, that are then tested on multiple populations. For example, exploration levels are predicted to be higher in species with variable food sources (Gosling & John, 1999), and neophobia is predicted to be greater in ecological generalists compared to specialists (Greenberg, 1983). By necessity, these hypotheses require ecological and environmental information, and hence lend themselves to studies of wild animals. Réale et al. (2007) suggest that inter-species comparisons could also be used to study functional relationships and trade-offs between traits, as well as the role of temperament in speciation.

Long-term studies of temperament in wild populations

In only two species have long-term studies been carried out within specific research groups that address multiple of Réale et al.'s (2007) steps in wild populations. These are the great tit and the bighorn sheep (reviewed in detail by Dingemanse & Réale, 2005; Groothuis & Carere, 2005; and see Quinn et al., 2009, for more recent work on great tits). Of these, only the great tit research considered the causes and effects of inter-population difference on temperament, and neither extended to consider inter-species comparisons. However, for at least one other species there are now enough data from a variety of researchers to address all of the steps.

The temperament of three-spined sticklebacks has been extensively studied, because the landmark study of Huntingford (1976) demonstrated that anti-predator behaviour and aggression were correlated in this species. This aggression–activity–boldness syndrome is heritable (Bell, 2005; Bell & Sih, 2007; Dingemanse et al., 2009). Boldness is positively linked to foraging success (Ioannou, Payne & Krause, 2008), but negatively to predation risk (Bell & Sih, 2007), demonstrating an effect of temperament on fitness. Inter-population comparisons have been integral to these studies. Not only does temperament differ between populations, being affected by both predator and habitat differences (Alvarez & Bell, 2007; Brydges et al., 2008; Dingemanse et al., 2009), but predation risk affects the strength of the relationship between temperament traits (Dingemanse et al., 2007). Predation risk affects temperament in this species both genetically and via behavioural plasticity (Bell & Sih, 2007; Dingemanse et al., 2009).

Larger datasets make it easier to identify multiple temperament axes, how they affect fitness and their interactions. But the specific advantages of long-term studies in wild populations are that they make it easier to quantify survival and lifetime reproductive success, the trade-off between these fitness measures, and how they relate to temperament variation. It also allows the identification of non-linear relationships, and this will allow the types of selection acting on temperament traits to be identified (Smith & Blumstein, 2008). For example, only with long-term studies can we identify the extent of spatial and temporal environmental

variability, and the evolutionary outcomes that this variability has on temperament in wild populations.

Lessons from human studies

Although this review seeks to stimulate further study of temperament in wild populations, it is also important to recognize that ecological and evolutionary studies of temperament can learn much from studies of captive animals, and indeed of humans. Human temperament has been extensively studied for many years, although the aims of these studies frequently differ from those on wild populations. Specifically, they rarely consider ultimate as compared to proximate explanations for temperament variability (Gosling & John, 1999; Gosling, 2001). However, evolutionary explanations are now being more widely considered in human studies (Nettle, 2006; Uher, 2008). Irrespective of this difference, animal studies stand to benefit from the multi-dimension approach of human studies, as well as the more rigorous use of definitions and more complex statistical analyses.

Human studies emphasize that there are multiple axes of temperament, for example extroversion, agreeableness and neuroticism, which may interact with one another (John, 1990). In contrast, animal studies often investigate only one type or axis of behaviour at a time, even though understanding temperament variation in adaptive terms will ultimately require the integration of behaviours and their effects on fitness and selection (Sih et al., 2004a,b; Dingemanse & Réale, 2005; Bell, 2007; Réale et al., 2007). One axis that is used frequently in animal studies is that of boldness-shyness. Boldness used to be an ill-defined term that incorporated risk taking across situations. As such, it could be argued to incorporate aspects of exploratory behaviour, and could be influenced by activity levels. However, these are now recognized as three separate axes, with boldness being specifically defined as an individual's reaction to risky, but not new, situations (Réale et al., 2007). The sophisticated, multivariate statistics of the human temperament literature (Sih et al., 2004b) will allow these axes, and their effects, to be determined for animal studies.

Conclusion

Although it is now well accepted that animals show consistent differences in behaviour, relatively few studies to date have studied temperament in wild animals. Furthermore, only a small subset of these has investigated the functional consequences of this behavioural variation in natural populations (Wilson et al., 1994; Dingemanse & Réale, 2005; Smith & Blumstein, 2008). This means that our knowledge of the effects of temperament on fitness and selection remain limited (Clark & Ehlinger, 1987; Wilson, 1998; Dingemanse & Réale, 2005; Smith & Blumstein, 2008). There are often large logistical difficulties in carrying out behavioural studies in the field, and these can be further complicated by the need to carry out repeat observations, and to take tissue samples for genetic and physiological studies. However, we stress the fact that there are also considerable benefits. The role of temperament in the local adaptation and evolution of populations and species can only be fully elucidated in the context of their natural ecology. Thus, we need to examine variation in temperament under natural conditions.

Data from captive animal studies can be informative, particularly about the genetic determination, and potential physiological control, of temperament. Nevertheless, integrating temperament studies fully into an ecological and evolutionary framework requires an understanding of environmental as well as genetic influences on temperament. Spatial and temporal variation in environmental factors may ultimately be the driving force behind the maintenance of temperament variability in wild populations (Wilson, 1998; Dingemanse et al., 2004). Perhaps surprisingly, because they are even further removed from studies of wild animals, much can also be learnt from human personality studies. Personality is a well-established and long-standing area of psychology with robust methodologies and sophisticated statistical analyses. The challenge for ecologists and evolutionary biologists is to draw information, techniques and approaches from these disparate areas into temperament studies on wild individuals and populations.

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