

# The Evolution of Animal Personality Variation

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**In many species of animals individual behaviour differs, yet is consistent over time and in an array of different environments; in other words, these animals display 'personality' variation. This may emerge not by chance, but, instead, is shaped by selective processes favouring individuals who display a differentiated behavioural phenotype. Indeed, personalities are known to affect important activities such as resource acquisition, survival and reproduction – which, cumulatively, impact an individual's fitness. We currently lack the insights and technology needed to fully characterise the genetics and physiology of most ecologically relevant behaviour; however, much can be gained by adopting an adaptive approach to consider the evolutionary processes that might have driven the emergence and maintenance of stable behavioural variation. Such an exercise will allow us to develop a priori hypotheses about the mechanisms underlying the behaviour, and to conduct powerful empirical studies examining how individualised behaviour impacts the life histories of a variety of species.**

## Introduction

For anyone who spends time watching animals, there is often a strong sense that, even within otherwise uniform populations of the same species, individuals differ predictably in their behaviour. Indeed, it is becoming increasingly evident that such stable interindividual variation – often referred to as 'coping styles' (Koolhaas *et al.*, 1999), 'temperament' (Réale *et al.*, 2000), 'behavioural syndromes' (Sih *et al.*, 2004) and, of course, 'animal

personality' (Schuett *et al.*, 2010) – is widely distributed across the animal kingdom (Smith and Blumstein, 2008). Prompted by Wilson's (1998) call for an evolutionarily motivated approach to studying biological variation at this scale, behavioural ecologists have recently put substantial research effort into developing this broad understanding of individual variation (for a recent review, see Bell *et al.*, 2009). One essential component of this work, and the main focus of this article, is an evaluation of the evolutionary processes that may underlie this apparently common feature of animal populations and individual behaviour. See also: [Animal Personality](#)

## What is animal personality?

At some level, it is intuitively obvious what personality is. Given our sociobiology, we, as humans, effortlessly cue in on individuality and individual behaviour patterns. This is reflected in the centrality of personality studies in treatments of human behaviour in the social sciences and humanities (Nettle, 2006). Nevertheless, psychological definitions of personality range from the vaguely broad ('individual differences within species'; Gosling and John, 1999) to the idiosyncratically human-specific ('those characteristics of individuals that describe and account for consistent patterns of feeling, thinking and behaving'; Pervin and John, 1997). However, these extremes are of limited value when considering patterns of individual variation in an evolutionary and ecological context. Thus, further elucidation is clearly required.

There are several types of phenomena that should be included within the scope of animal personality studies in order to elucidate their evolutionary function. First and foremost, investigators must consider behavioural variation amongst individuals within otherwise homogenous populations or groups of the same species. Crucially, however, researchers must also consider the patterns of behaviour that individuals exhibit over some portion of their lifetimes and/or across the different biological contexts they face (e.g. foraging, mating, socialising, etc.) as a hallmark of personality is the relative consistency of

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individual behaviour over some portion of a life history (Bell *et al.*, 2009). Many existing studies on animal personality achieve both of these goals. By achieving this, they go beyond studying interindividual variation generated by any specific proximate mechanisms (e.g. genetic coding); thereby avoiding potential confusion over levels of explanation (Tinbergen, 1963) by focussing on observable patterns of behaviour per se. In other words, these sorts of animal personality studies encompass variation that is genetically driven, while also considering interindividual variation that (1) involves substantial behavioural plasticity, (2) is not necessarily stable over an entire lifetime and (3) depends on social status or condition (Dingemanse *et al.*, 2010). **See also:** [Life History Theory](#)

## Why is animal personality interesting from an evolutionary perspective?

Although the patterns of behavioural variation that characterise personality appear to be widespread within animal populations, it may not be entirely clear why evolutionary accounts of such phenomena are necessary. After all, all biological systems are characterised by mutation and stochastic influences during epigenetic development – the two factors that are responsible for differences between individuals. However, the consistency with which we have observed interindividual differences in behaviour suggests that this variation drives differential patterns of survival and reproduction, and is therefore a target for selection. Indeed, this seems to be the case in a wide range of species (Smith and Blumstein, 2008) studied in both the lab (e.g. Schuett *et al.*, 2011) and field (e.g. Dingemanse *et al.*, 2004; **Figure 1**). **See also:** [Natural Selection: Introduction](#)

One notable example is the great tit (*Parus major*), a species in which individuals exhibit consistent differences in exploratory behaviour (Dingemanse *et al.*, 2004). Interestingly, the fitness impacts of great tit personality are known to vary depending on both year and sex. Researchers have found that this stems at least partly from fluctuations in resource availability and dominance interactions. Males are dominant over females and therefore regulate their access to food – a situation that can place females at a disadvantage in the years when resources are scarce. Thus, tits with ‘fast explorer’ personalities are successful when environmental conditions favour competitiveness; however, when the key, sex-specific resource is not limiting, hypercompetitiveness is likely to be costly, and ‘slow explorers’ appear to be favoured (Dingemanse *et al.*, 2004). **See also:** [Interspecific Competition](#)

Another reason to believe that evolutionary accounts of animal personality are important is the stability of individual behaviour at the heart of the phenomenon. For individual animals to behave consistently, they must exhibit relatively low levels of behavioural flexibility as conditions vary, or in different contexts. This suggests that individuals will behave in a less-than-perfectly efficient manner in at least some circumstances (Sih *et al.*, 2004). Indeed, exactly this pattern has been observed in the larvae of streamside salamanders (*Ambystoma barbouri*). In predator-free environments, active larvae outcompete their rivals and so have higher levels of success; however, when this same behaviour is displayed where predators are present, the larvae are more conspicuous and therefore suffer higher mortality rates (Sih *et al.*, 2003). If such insidious behavioural inefficiencies are a common feature of animal personality, this begs the question as to how animal personality, and, more precisely, behavioural stability, can persist over evolutionary time; instead, it may seem more



**Figure 1** Species in which personality variation has been linked with fitness. Top row, from left to right: Great tit (*Parus major*), southern dumpling squid (*Euprymna tasmanica*), three-spined stickleback (*Gasterosteus aculeatus*), bighorn sheep (*Ovis canadensis*). Bottom row, from left to right: zebra finch (*Taeniopygia guttata*), water strider (Heteroptera) and guppy (*Poecilia reticulata*). Images reproduced courtesy of Alastair Stewart, David Mitchell, Katie McGhee, Jim Cummins, Jan Stipala, Ingela Danielsson/Jens Rydell and Gregory Grether, respectively.

likely for personalities to emerge as a (possibly transient) feature of animal systems resulting from localised constraints on behaviour that pause evolutionary trajectories at local peaks in the adaptive landscape en route to their stable global optima (Hammerstein, 1998).

Given the possibility that personality variation reflects the widespread action of constraints on behaviour, students of the evolution of animal behaviour must consider the role of proximate factors in more depth than is typical of their field (Duckworth, 2010). Indeed, perhaps one of the most important consequences of the burgeoning interest in animal personalities is that it is forcing behavioural ecologists to confront an implicit notion that behaviour is infinitely flexible until proven otherwise. However, the concept of systemic limitations to behavioural responses should not really be surprising, as behaviour merely reflects what is possible for animals given their morphologies and physiologies (Duckworth, 2010); behaviour should be constrained in ways that are similar to those acting on an individual's other phenotypic traits. In fact, a holistic, Tinbergenian perspective (Tinbergen, 1963) suggests that behaviours in different contexts (e.g. foraging, mating, etc.) should be analysed as a suite of 'correlated traits' (Sih *et al.*, 2004), an outlook that is in line with recent approaches to thinking about the evolution of phenotypic traits in general (e.g. Réale *et al.*, 2010).

The 'correlated traits' view of the behavioural phenotype as a whole, along with the purported fitness consequences of personality differences, suggests a central role for animal personality in determining the evolutionary dynamics of behavioural phenotypes in general. The widespread existence of animal personality suggests that behavioural traits are interrelated; this, in turn, indicates that simple global optima of the sort typically envisaged by theoretical evolutionary biologists (particularly behavioural ecologists) may not be realistic evolutionary outcomes. Instead, more complex adaptive landscapes need to be considered. Indeed, in formal analyses of how fitness surfaces are impacted by interactions between traits, landscapes go from smooth surfaces with single global peaks (no interactions) to landscapes with a very large number of small, widely dispersed peaks; the diminutive size of each peak reflects the fact that multiple traits interact with each other to determine fitness (Kauffman, 1993). In other words, it is increasingly apparent that animal personality results in complex behavioural fitness landscapes arising from non-linear relationships between components of each behavioural trait, as well as from interactions between such traits (Gilchrist and Kingsolver, 2001). Such personality-driven landscapes mean that fully characterised evolutionary accounts of behavioural evolution will often require approaches that are not limited solely to pure optimisation and game theory considerations, but also include the details of the composite trait interactions and their inheritance (Gilchrist and Kingsolver, 2001).

Nevertheless, it is important to adopt a deductive approach to hypothesising about animal personality, especially as we are a long way from being able to fully

characterise the genetics and physiology of most ecologically relevant behaviour. Until these goals are possible, adopting an explicitly adaptive approach to thinking about the evolution of animal personality can offer a rigorous means of generating testable hypotheses. Moreover, the burgeoning empirical interest in animal personalities offers the opportunity to think, in detail, about how evolutionary processes might shape integrated phenotypes and about what such adaptive integration might look like. This, in turn, will allow us to posit a priori hypotheses about the mechanisms underlying the behaviour (e.g. McNamara and Houston, 2009). Questions arising from such deductive considerations include: What maintains between-individual variation? When is within-individual consistency adaptive? Why should individual behaviour be correlated across contexts? Why do we see so much individual behavioural specialisation? The following text briefly summarises current thought on answers to such questions from an evolutionarily adaptive perspective. **See also:** [Adaptation and Constraint: Overview](#)

## Factors selecting for interindividual variation within populations

There are a wide range of evolutionary processes that can generate variation amongst individuals within populations (Bergstrom and Godfrey-Smith, 1998). The generation and maintenance of such variation has been examined by evolutionary biologists since Darwin and Wallace first articulated their ideas about evolution by natural (and sexual) selection (Fisher, 1930). Nevertheless, it is important to provide a brief overview here, if only to highlight that, though such processes are necessary, they are by no means sufficient to explain the evolution and maintenance of animal personality variation.

## Mutation and stochasticity

Perhaps the most ubiquitous sources of individual variation stem from the randomness inherent in biological processes. For behaviour (as for many phenotypic traits), this randomness generates interindividual variation at two fundamental biological levels: behavioural inheritance and development. On the one hand, as for any genetically controlled trait, the balance between mutation and selection determines heritable behavioural variation around the adaptive 'foci'. Moreover, phenotypic variation is determined by the sum of genetic variation and environmental influences, many of which can be fundamentally stochastic in nature (Falconer and Mackay, 1996). In this way, the existence of behavioural differences among individuals within a population can, in principle, be attributed to chance and have little evolutionary or ecological importance (beyond generating the necessary heritable variation upon which selection can act). For many years, this was the prevailing, often implicit, interpretation of the kind of

behavioural variation that is now the focus of modern animal personality studies (Wilson, 1998). However, as has been pointed out repeatedly (Wilson, 1998; Dall *et al.*, 2004; Sih *et al.*, 2004; Smith and Blumstein, 2008; Schuett *et al.*, 2010), the nonrandom distribution of such variation along particular axes undermines mutation–selection balance and developmental stochasticity as sufficient explanations for the phenomenon of animal personality. **See also:** [Environmental Stochasticity](#)

## Strong tradeoffs

Even in constant environments, strong selection pressures can generate a range of different phenotypic states if they offer equivalent fitness payoffs. Indeed, it has been suggested that growth rates are particularly susceptible to being ‘equivalated’ by selection, given that there are often strong tradeoffs between (fast) growth and mortality rates (Mangel and Stamps, 2001): To grow quickly, individuals must consume resources at high rates, which inevitably increases their activity levels and concomitant risks of exposure to natural enemies and other hazards (Lima and Dill, 1990). Indeed, both the tradeoffs themselves and stochastic variation amongst individuals in the perception of danger can result in more or less flat fitness landscapes around the adaptive growth rate optima (Mangel and Stamps, 2001), or can generate disruptive selection (Wolf *et al.*, 2007).

Interestingly, much of the variation that is being reported as ‘animal personality’ involves behavioural responses to risk and ecological uncertainty (e.g. exploratory behaviour and learning), and is increasingly being linked to variation in individual growth rates and the life history strategies they engender (Biro and Stamps, 2008; Wolf *et al.*, 2007; Réale *et al.*, 2010). Nevertheless, unless the differences in growth rates (i.e. life history trajectories) are reinforced by the optimal behaviours with which they are associated, the functional equivalence of a range of growth rates per se will not explain the persistence and stability of particular growth rate-induced behavioural tendencies (McElreath *et al.*, 2007); this is because the asset protection should be associated with a state-dependent negative feedback on behaviour adjustment.

## Spatiotemporal fluctuation

Adaptive behaviour can often differ amongst individuals within populations because different things are selected for at different times and in different places within the larger niche that a population occupies. Indeed, temporal fluctuation in optima is essentially the rationale promoted by Dingemanse *et al.* (2004) to explain the maintenance of differences in exploratory behaviour in their great tit population (see above). However, again, the fact that optima vary across a population’s niche and/or over time does little to explain, by itself, why individuals should persist in pursuing any particular optimum over substantial portions of their life histories (Dall, 2004). Indeed, the

existence of varying optima within a population’s niche is often expected to lead to adaptive phenotypic plasticity and condition-dependent behaviour (West-Eberhard, 2003) or (particularly for intergenerational variation) probabilistic ‘bet-hedging’ (Hopper *et al.*, 2003), rather than the coexistence of a mixture of specialised behavioural phenotypes that epitomise animal personality variation.

## Condition and state dependence

The optimal action that an animal can take rarely remains constant from one moment to the next. On the face of it, this suggests that selection should favour animals that constantly adjust their behaviours in real time. In models of animal behaviour, it is often useful to account for the conditions that explicitly affect the payoffs of a given behaviour, then track how these payoffs change both as a function of what the animal does and, independently, as a function of how the environment changes (Houston and McNamara, 1999). An animal’s ‘state’ comprises those factors that are determined by past behaviour and also determine future behaviour; thus, adaptive behaviour is often said to be state dependent (Houston and McNamara, 1999). Adopting such an outlook makes it easy to see why individuals are likely to differ at any one moment in time, as individual state often varies as a function of prior experience and localised environmental conditions.

However, condition dependence and state dependence alone cannot account for the stability of animal personalities, as individual states and environmental conditions are likely to vary continuously over an animal’s lifetime (Dall *et al.*, 2004). Despite this, condition dependence has been evoked as an explanation for the adaptive coexistence of stable behavioural strategies in specific contexts, notably in the case of alternative reproductive tactics within the sexes (e.g. Gross, 1996). It is difficult to extend such reasoning to explain the widespread existence of personality variation, as, by this logic, preexisting variations in morphology or growth trajectories (which are typically thought of as unchangeable over behavioural timescales) are responsible for the differences in state or condition that determine optimal behavioural tactics (see below for further discussion). Thus, the stability of the alternative tactics does not require specific explanation. In contrast, a key aspect of animal personality is that individual behaviour varies stably within groups of animals that appear otherwise similar; in other words, it is apparently unlinked to obvious differences between individuals, such as those within sex or age classes, or within morphotypes (Wilson, 1998; Sih *et al.*, 2004).

## Negative frequency dependence

Since the 1970s, behavioural and evolutionary biologists have recognised that competition for limiting resources can often select for mixtures of tactics to be expressed within populations (Maynard Smith and Price, 1973). This can occur when the increasingly common use of a tactic or

strategy renders it less effective, thereby resulting in a negative relationship between fitness and the expression of this strategy (i.e. negative frequency dependence). This is exemplified by the Hawk–Dove game, the archetypal evolutionary scenario that introduced game theory to evolutionary biology (Maynard Smith and Price, 1973). The game predicts a stable mixture of two tactics (in this case, aggressive ‘hawk’ behaviours and pacifist ‘Dove’ behaviours) at evolutionary equilibrium; relative expression levels of these two tactics depend on the balance between the costs and benefits of fighting (Maynard Smith and Price, 1973). Nevertheless, by itself, such negative frequency dependence cannot explain the evolution and maintenance of personality variation, as it does not distinguish between evolutionarily stable equilibria that are mixtures of ‘pure’ strategies within populations (e.g. some individuals always play Hawk while others always play Dove) from populations of individuals that play each tactic probabilistically (the so-called mixed evolutionarily stable strategies) (Bergstrom and Godfrey-Smith, 1998; Dall *et al.*, 2004). **See also:** [Evolutionary Game Theory](#); [Selection: Frequency-dependent](#)

## Factors selecting for individual behavioural specialisation

Animal personality can also be thought of as behavioural specialisation at an individual level (Dall *et al.*, 2012). Great tits, for example, may specialise in either quickly or slowly exploring their environments; the choice between these two behaviours may mean the difference between gaining access to limited resources and being outcompeted, respectively (as discussed in more detail above). The evolution and maintenance of these different behavioural phenotypes can be driven by multiple factors. When personalities function as a signal of quality (or any other desirable intrinsic property), they can be selected for directly (Schuett *et al.*, 2010). However, when such behavioural consistency reflects the fortuitous outcome of consecutive state-dependent decisions where animals are expected to behave in an optimal way, indirect selection may occur (Wolf *et al.*, 2007).

## Specialisation/generalisation tradeoffs at an individual level

Why should generalists, or animals that exploit a wide range of resources, ever specialise; and, conversely, why should specialists fail to develop flexibility in their sampling and searching behaviours? These questions form the crux of the specialisation/generalisation conundrum, and are equally pertinent in any consideration of how animal personalities evolved and are maintained. Theoretical work has shown that the size of an animal’s foraging niche (e.g. whether it is a specialist or generalist) is determined by the costs of environmental and physical constraints (Dall and

Cuthill, 1997), mediated by the fact that most animals are limited in the amount of attention they can commit to any one of the many distinct demands being continuously made on their cognitive processes (Dukas, 2002). Each animal’s behaviours should be optimised for success within the boundaries set by these two major factors. Thus, to understand the evolution of behavioural consistency, it is crucial to determine the costs and benefits of specialism in an animal’s socioecological conditions. In general, specialisation occurs as a result of two major processes: positive feedback loops and the benefits of consistency (i.e. predictability) *per se*.

## State-dependent feedback

It has recently been proposed that consistent behavioural differences between individuals may have coevolved with a tradeoff between current and future reproduction (Wolf *et al.*, 2007). Individuals with low expectations for future reproduction should proactively attempt to maximise energy acquisition and reproduction opportunities, whereas those with high expectations might be expected to act more in a more subdued and cautious manner. According to the asset protection principle (Clark, 1994), energy acquisition by ‘low-expectation’ individuals should result in behavioural modifications aimed at protecting their new assets; thus, resources can drive a negative feedback loop that decreases the incidence of risk-taking behaviours over time. However, additional behavioural modifications would be expected as a result of further changes to asset levels (either positive or negative); this indicates the need for a ‘positive feedback scenario’ in which gaining an asset results in an improved ability to protect it (McElreath *et al.*, 2007) and in behavioural consistency over time.

Indeed, recent theoretical work has shown that this sort of positive feedback scenario could promote consistent behavioural differences between individuals. Specifically, a model of state-dependent safety revealed that if higher-quality individuals – those with more energy reserves, a larger size, or better condition – were better equipped to escape predators, then state-dependent variations in this ability would be associated with the long-term maintenance of different personality types (Luttbeg and Sih, 2010). Similar patterns would be expected for additional state-dependent ‘skills’, such as foraging ability or competitiveness with rivals; as in the predator avoidance model, the benefits of remaining active would continue to increase over time, and so outweigh the benefits of adopting a new behaviour in order to focus on merely protecting assets.

Behavioural variation should also result from state-dependent energy demands. For example, when individuals of different conditions (or any energetic state) forage in pairs or groups, lower-state animals should be bolder in their search of foraging opportunities, as they have less to lose by making themselves conspicuous. Higher-state individuals – who should consistently display a better condition – are expected to follow the lower-state

'pioneers' and demonstrate a greater willingness to leave the foraging patches. Lower-state individuals, on the contrary, should generally remain in a poorer condition and leave foraging areas only when forced (Dall *et al.*, 2004).

Finally, both learning and responsiveness are associated with positive feedback mechanisms that could drive animal personality variation. Learning is a process that typically improves an individual's ability as it gains experience; thus, behavioural differences are expected between learners and nonlearners. Likewise, responsiveness to environmental stimuli appears to be less costly to individuals that have previously been responsive; this should facilitate the development and maintenance of at least two personality types: responsive and unresponsive (Wolf *et al.*, 2008).

### Adaptive packaging into suites of traits

As indicated above, characteristics associated with 'state' often involve aspects of physiology and of morphology, which are generally regarded as proximate mechanisms driving particular behaviours. Rather than viewing behaviour simply as a result of these mechanisms, however, it is more parsimonious to infer that behaviour, physiology and morphology have coevolved (Sih *et al.*, 2004): Not only do physical characteristics shape behaviour, but behaviour may also impact ongoing development and plasticity. This is the logic behind the pace-of-life syndrome hypothesis, which posits that behavioural traits may have coevolved with both physiology and life history (metabolism and life history, specifically) along a life continuum – one end of which is populated by animals that have a slow pace of life, and the other end of which features animals with a faster pace (Réale *et al.*, 2010).

### Adaptive consistency

Behavioural consistency can be thought of as the outcome of evolutionary processes that generate a mixture of flexible and nonflexible phenotypes; or, in other words, different personalities. However, personalities might also result from direct selection, such that individuals with a higher behavioural consistency experience higher fitness (Schuett *et al.*, 2010).

The costs and benefits of behavioural flexibility are much more poorly understood than those of phenotypic flexibility (DeWitt *et al.*, 1998). This likely stems from the fact that the benefits of behavioural flexibility are obvious, whereas its costs have historically been assumed to be negligible. However, it is possible that behavioural phenotypes are acquired during a developmental period early in life, after which they become more or less 'fixed'; this putative process is similar to that observed in juvenile birds learning to sing (see Chapman *et al.*, 2010). A developmental approach to animal personality variation is urgently needed in order to elucidate whether and how behavioural flexibility varies throughout an individual's life, and whether some aspect of this process, or the resulting phenotype, is under selection (Duckworth, 2010;

Stamps and Groothuis, 2010). If the results of studies on phenotypic plasticity are any indication of the patterns we might expect from work on behavioural plasticity, we are likely to find costs and benefits associated with strong genetic determinism (e.g. Korsten *et al.*, 2010) and/or information acquisition, processing and availability (Dall and Cuthill, 1997). **See also:** [Neural Control of Birdsong](#)

The development and maintenance of behavioural consistency may also be influenced by social interactions (Wolf *et al.*, 2011; McNamara *et al.*, 2009). An individual could benefit greatly from responding to the behaviour of a conspecific that is known to be predictable and consistent over time; payoffs might include improved predator avoidance or increased access to resources. On the contrary, responses to unpredictable conspecifics could have a number of costs, including inaccurate socially mediated decisions or increases in aggressive encounters (e.g. Dall *et al.*, 2004; Wolf *et al.*, 2011). In fact, behavioural consistency may also provide conspecifics with important information about an individual's genetic quality. Assuming that there are some costs associated with the expression of a particular personality, these costs should be particularly hard to bear for individuals with poor genetic quality; thus, these individuals should be less consistent in their behaviour. Animals with more repeatable behavioural patterns, then, are those with a higher genetic quality. In other words, animal personalities can act as a signal that can be appraised by conspecifics interested in evaluating an individual's quality. This is likely to be particularly relevant in a mate-choice context, where the potential partners wish to optimise the genetic quality of their mates, or where the reproductive partner's behavioural phenotype is likely to influence reproductive success (and, therefore, fitness; e.g. Schuett *et al.*, 2011). Indeed, studies of songbirds have found that the consistency of a male's vocal performance was a good predictor of his dominance status, reproductive success and likelihood of being cuckolded (e.g. Botero *et al.*, 2009). Although further studies are needed to more completely assess the costs of vocal performance consistency, these preliminary findings indicate that behavioural consistency can be correlated to some intrinsic quality that may be a target during the mate-choice process. These may be particularly useful in monogamous species where reproductive partners frequently interact during reproductive events, and where each member of the pair differs in its ability to raise the young. In such cases, fitness outcomes will vary depending on the combined behavioural phenotype (Schuett *et al.*, 2011; Mariette and Griffith, 2012). Thus, choosing individuals should benefit greatly from a reliable signal of their potential mate's behavioural phenotype (e.g. Schuett *et al.*, 2011). **See also:** [Sexual Selection](#)

### Conclusions

Although it is tempting to view behaviour as different from other animal characteristics (e.g. morphology,

physiology), it is increasingly clear that this inclination is unfounded. Like these other traits, behaviour – or, in the case of animal personality, suites of behaviours – may be shaped by evolutionary processes that favour individuals displaying a particular phenotype. Although variation in particular behavioural traits may emerge merely by chance, rule-based dynamics, such as those emerging from state-dependent behaviour, can maintain and even increase the expression of distinct personalities. Indeed, behavioural conundrums such as the ‘lek paradox’ may be explained by approaches that take into consideration the fact that strong selection can favour variability.

Personality research has underscored the evolutionary importance of the social component of animal environments. Further, these studies have revealed that behaviour can be viewed as a snapshot of an individual’s life history strategy. As this is the only perspective from which a particular strategy’s adaptive value can be assessed, work on personalities has provided vital information about the relationships between behaviour, whole phenotype, fitness and evolutionary processes in general.

As important as this work has been, perhaps the biggest contribution of personality research is that it allows us to go beyond investigating as to which factors explain the average behavioural type in a given situation, and instead explore more complex and fundamental questions, such as (1) Why might some individuals of a species consistently display different behaviours than observed in their conspecifics? (2) Why are there correlations between some types of behaviours (boldness and aggressiveness, for example)? (3) What conditions allow for the maintenance of multiple behavioural suites within a single population? and (4) What factors promote the evolution of behavioural stability? Answers to these questions (and more) will illuminate the connections between genotype, phenotype and the environment, and advance our understanding of the evolutionary forces at work on the organisms around us.

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