

# Animal personalities: consequences for ecology and evolution

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**Personality differences are a widespread phenomenon throughout the animal kingdom. Past research has focused on the characterization of such differences and a quest for their proximate and ultimate causation. However, the consequences of these differences for ecology and evolution received much less attention. Here, we strive to fill this gap by providing a comprehensive inventory of the potential implications of personality differences, ranging from population growth and persistence to species interactions and community dynamics, and covering issues such as social evolution, the speed of evolution, evolvability, and speciation. The emerging picture strongly suggests that personality differences matter for ecological and evolutionary processes (and their interaction) and, thus, should be considered a key dimension of ecologically and evolutionarily relevant intraspecific variation.**

## Personality differences in animal populations

The study of animal behavior has undergone a major shift during the past decade. Individual differences in behavior that traditionally were considered as noise, not requiring further investigation, have become a key target of research [1]. Two findings promoted this shift. First, behavioral differences tend to be highly structured, that is, both stable over time and correlated across different situations and contexts [2,3]. Second, such structured behavioral differences are a common feature of animal populations, occurring in a diverse range of species across the animal kingdom [4–6]. Behavioral differences that are maintained through time and across contexts are termed ‘personalities’ in humans and, analogously, the term ‘animal personalities’ has been adopted in the literature [4] (see Glossary). The emerging notion that within-population behavioral differences are the expression of differences in highly structured behavioral types promoted an explosion of empirical and conceptual research. Much of this research has focused on the existence and structure of personalities [3,4,6] and the proximate and ultimate causes of personality differences [7–13]. As a result, a substantial body of knowledge about the occurrence, form, and causes of animal personalities has accumulated (Box 1). However, surprisingly little attention has been paid to the ecological and evolutionary consequences of personality differences. Do personalities matter in this respect?

## Consequences of individual variation

There is growing awareness that the amount and structure of within-population variation can substantially affect key ecological and evolutionary processes, and their interaction. Evolutionary biologists realize that not only is standing genetic variation the substrate of evolution, but also the degree and patterning of genetic and phenotypic variation can determine the direction and outcome of natural selection [14,15]. In parallel, ecologists increasingly recognize individual variation as an important factor affecting intra- and interspecific competition and the structure and dynamics of ecological networks [16–21]. Moreover, by speeding up evolution, within-population variation also affects the interplay of ecology and evolution. In the presence of variation, ecological and evolutionary processes often proceed at similar timescales, leading to an intricate and often counterintuitive interaction of both processes [22].

Until now, most research on the consequences of within-population variation focused on genetic variation [16,19,22] and differences in resource use [17], largely

## Glossary

**Animal personalities:** the phenomenon that individuals differ systematically in their behavioral tendencies; these differences are consistent over time (i.e., individuals that tend to score higher on a particular behavioral axis tend to score higher on that axis at later points in time) and correlated across different situations and contexts (e.g., individuals that tend to be more aggressive towards conspecifics also tend to be bolder in novel environments than less aggressive individuals).

**Behavioral and/or personality type:** a particular combination of behavioral tendencies forming part of a behavioral syndrome.

**Behavioral syndrome:** a suite of correlated behavioral tendencies in different situations and contexts; examples are the aggressiveness-boldness syndrome (referring to the correlation between intraspecific aggressiveness and boldness in novel environments) and the pace-of-life syndrome (referring to the correlation between metabolic, hormonal, and immunity traits favoring either fast and early reproduction at the expense of longevity, or vice versa).

**Euler-Lotka Equation:** an implicit equation describing how, in populations with overlapping generations, the *per capita* growth rate of the population depends on demographic parameters such as age- or state-dependent survival and fecundity.

**Jensen's inequality:** mathematical rule stating that, for a convex function  $f(x)$ , applying this function to the mean  $\bar{x}$  of some variables  $x_1, x_2, \dots$  yields a lower value than taking the mean  $\bar{f(x)}$  of  $f(x_1), f(x_2), \dots$ :  $f(\bar{x}) < \bar{f(x)}$ .

**Lande's multivariate selection equation:** a generalized version of the breeder's equation of quantitative genetics describing how the mean (multivariate) phenotype  $\bar{z}$  will change under selection; one version of the equation is  $\Delta \bar{z} = \bar{w}^{-1} \mathbf{G} \boldsymbol{\beta}$ , where  $\bar{w}$  is the mean fitness of the population,  $\boldsymbol{\beta}$  is the selection gradient, and  $\mathbf{G}$  is the G-matrix of the population (i.e., the matrix of additive genetic variances and covariances).

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**Box 1. Animal personalities in a nutshell**

The term 'animal personalities' refers to systematic and structured within-population differences in behavioral tendencies, where these tendencies are stable over some period of time and where the behavior in one situation or context is correlated with the behavior in other situations or contexts. For example, many organisms, including fish, birds, and rodents, exhibit an aggressiveness–boldness syndrome [6]: some individuals tend to be more aggressive than others (variation), these differences remain stable over longer periods of time (time consistency), and aggressiveness is correlated with boldness in that more aggressive individuals tend to be bolder in response to predators than less aggressive individuals (correlations across contexts). In populations with personalities, individuals are said to have a personality or behavioral type (e.g., more aggressive types vs less aggressive types), behaviors that are involved in personality differences are termed personality traits (e.g., aggression and boldness), and suites of correlated traits are termed a 'syndrome' [2].

Animal personalities have been reported for a range of animal species across the animal kingdom, including mammals, fish, birds, reptiles, amphibians, arthropods, and mollusks [4,6]. Consistent differences have been reported for a large number of behavioral tendencies [3–6], including aggressiveness, boldness, activity level,

cooperativeness, fearfulness, dispersal tendency, exploration tendency, docility, impulsivity, sociability, and responsiveness to environmental stimuli. Well-known syndromes found in various organisms are the aggressiveness–boldness syndrome [6], the pace-of-life syndrome (Implication 1, Table 1), the dispersal syndrome (Implication 4, Table 1), and coping styles [59].

On a proximate level, personality differences can often be understood in terms of the behavioral architecture, that is, the genetic, physiological, and cognitive systems underlying behavior. Personality differences are, for example, systematically associated with differences in metabolism [7,89], stress physiology [59], and strength of cerebral lateralization [90]. On an ultimate level, key questions are why behavioral differences persist in the face of selection, and why behavior is organized in syndromes rather than being more flexible. Several explanations have been put forward, and various evolutionary models demonstrate how personality differences can emerge and persist [7–13].

Personality differences might reflect genetic differences, environmental-dependent phenotypic plasticity, or a combination of both factors. Genetic studies find that behavioral types are moderately heritable as narrow-sense heritability estimates range between 10% and 40% [5,91].

neglecting behavioral differences (Box 2) and, in particular, personality differences. The studies investigating the consequences of variation in behavioral types are few and focus on a limited number of issues. However, the importance of such variation became evident in all areas where it was addressed explicitly (see also [21]); for example, host–parasite interactions [23,24], epidemiology [25], dispersal and invasion biology [26–28], and fisheries management [29,30].

In this review, we aim to provide a comprehensive inventory of the potential consequences of personality differences for ecological and evolutionary patterns and processes. We discuss 14 implications, which are summarized in Table 1. For each implication, we provide a link between personality variation and the ecological or evolutionary issue of interest, outline basic mechanisms, and briefly discuss theoretical predictions and empirical evidence (Box 3 provides a detailed discussion of one particular example).

**Implications of personality differences for ecology and evolution***Implication 1: life history and demography*

Differences in behavioral type are systematically associated with differences in life history, that is, the mortality and fecundity profile of individuals [11,31,32] (Box 2). This is of evolutionary relevance given that life-history parameters are key determinants of fitness. The association between behavioral type and life history arises in at least three ways. First, traits such as boldness, aggressiveness, activity, or dispersal tendency are often directly related to mortality risks and/or fecundity [11]. Second, different behavioral types often find themselves in different habitats (Implication 5), facing different resource densities, competitors, predators, and parasites, which all affect mortality and fecundity. Third, personalities often seem to be selected as part of a pace-of-life syndrome [12,31,33], reinforcing mortality and fecundity differences.

**Box 2. Behavioral variation and other forms of individual variation**

A surge of recent research points to the importance of intraspecific variation for ecological and evolutionary processes [14–22]. Most of this work focuses on genetic variation or differences in resource use. By contrast, the consequences of individual variation in behavior have received relatively little attention from ecologists and evolutionary biologists. This is surprising given that behavior is a key factor mediating the interactions of individuals with their environment [74,92]:

- The environment of an individual is, to a large extent, determined by the behavior of this individual, for example, as a result of dispersal and migration, movement patterns, habitat choice, feeding strategy, predator avoidance, mating strategy, or social behavior. Accordingly, behavior affects issues such as the spatial distribution of populations, resource exploitation patterns, and social interaction structures. Moreover, given that the environment of an individual determines the selection pressures acting on the whole phenotype, behavior can act as a 'pacemaker' of evolution for non-behavioral traits (e.g., life history, physiology, and morphology);
- Behavior is an important component of the immediate response of an individual to its environment. Accordingly, behavior is crucial for

understanding how populations respond to environmental change, thus affecting issues such as population stability and persistence. Moreover, behavioral responses can both slow down evolution (if individuals are shielded from novel selection pressures by evasion behavior) and speed up evolution (if individuals are exposed to novel selection pressures).

Behavioral variation is often associated with non-behavioral phenotypic variation (e.g., morphology [18], physiology [7,31,59,89], life-history characteristics [11,31,32], or cognition [90]). Behavioral variation might often be the cause of correlated non-behavioral variation, given that different behavioral types face different environments exerting different selection pressures on all aspects of the phenotype. In other cases, behavioral variation might be the result of non-behavioral variation, for example if the aggression level of an individual is made dependent on the resource-holding potential of the individual or if the activity level of an individual reflects its metabolic rate. However, in many cases, the causation of correlated behavioral and non-behavioral variation is not unidirectional but reciprocal, involving mutually reinforcing feedback loops between behavioral and non-behavioral traits [9,53].

**Table 1. Ecological and evolutionary implications in a nutshell<sup>a</sup>**

Implication	Aspect	Implications of BD	Mechanisms	Selected refs
1	Life history and demography	BD is associated with variation in demographic and life-history parameters; this variation affects fitness and population growth rate	Differential use of resources and environment; behavioral types often reflect pace-of-life syndrome; Jensen's inequality	[11,12,31]
2	Population density and productivity	BD tends to enhance the carrying capacity and productivity of a population	Competition avoidance; mutual facilitation; synergism due to behavioral complementation and division of labor	[19,35,36]
3	Stability, resilience, and persistence of populations	BD tends to enhance population stability, resilience, and persistence	Averaging effect; portfolio effect; insurance effect	[29,41,42]
4	Dispersal, colonization, and invasion	Dispersers and/or colonists, and/or invaders are a non-random sample; the mix of BT is crucial for establishment in new habitat and, hence, for the stability and persistence of a metapopulation	Dispersal syndrome; invasion syndrome; insurance effect	[26–28,36,43]
5	Distribution within habitats	BD induces spatial pattern formation, affecting evolutionary dynamics, population dynamics, and the interaction with other species	Differential movement patterns; non-random distribution of BT in space; non-random interactions among BT	[35,44,46,100]
6	Transmission dynamics: disease and information	BD affects crucial epidemiological parameters, often leading to rarer but more explosive outbreaks. Similar principles apply to the spread of information	Variation in contact number, contact rate, susceptibility (ability to acquire information), and infectiousness (ability to spread information)	[23,25,48,49]
7	Social evolution	BD changes the direction and outcome of social evolution	Mutual feedback between social responsiveness and consistency; diversity begets diversity; partner choice; handicap principle	[15,54–57]
8	Speed of evolution and adaptive potential	BD can speed up evolution by orders of magnitude, allowing rapid adaptation to environmental change	Instantaneous availability of 'adaptive' variation, rather than mutation limitation	[14]
9	Constraints on adaptive evolution	Behavioral correlations can retard adaptive evolution and prevent fitness peaks being achieved	Lande's multivariate selection equation; pleiotropic effects; constraints on the physiological architecture of behavior	[6,63,64]
10	Evolvability	Behavioral correlations can enhance the capacity of a population to evolve solutions to novel ecological challenges	'Pre-adapted' correlation structures favoring the production of well-integrated phenotypes	[65,66]
11	Eco-evolutionary dynamics	In the presence of BD, ecological and evolutionary dynamics might occur at similar timescales, often leading to qualitatively new kinds of (non-equilibrium) dynamics	Rapid evolution due to BD (Implication 8); non-equilibrium dynamics due to spatial segregation and strong feedbacks	[22,67,70,73]
12	Speciation	BD can facilitate speciation in a multitude of ways; e.g., by contributing to the divergence of incipient species, by generating the conditions for competitive speciation, and by acting as a 'magic trait'	Rapid evolution associated with BD (Implication 8); range expansion and settling in new habitat facilitated by BD (Implication 4); effects of BD on intensity of disruptive selection; association between ecological and mating traits in behavioral syndromes	[74,76,79]
13	Species interactions	BD affects both the interaction dynamics and the coevolution of species; might promote the stability and persistence of species interaction networks	Coexistence fostered by differences in competitive ability; BD causing increased connectivity and decreased interaction strengths in species networks	[17,21,81–83]
14	Community structure and ecosystem processes	BD can affect primary productivity, nutrient fluxes, and decomposition rates, as well as the composition and species diversity of food webs and other communities	Cascading effects transcending from the species and species interaction level to the community and ecosystem level	[86–88]

<sup>a</sup>Abbreviations: BD, behavioral differentiation; BT, behavioral types.

As well as determining fitness, life-history profiles in a population also determine key demographic parameters, such as the age distribution and sex ratio of the population. Via relationships such as the Euler–Lotka equation [34], these parameters directly affect the population growth rate. It is important to realize that predictions of population growth rates can be misleading if they are only based on average life-history characteristics and do not take

variation into consideration (see the discussion of Jensen's inequality in [17]).

#### *Implication 2: population density and productivity*

Behavioral types often differ systematically in activity patterns, habitat use, diet preferences, and foraging and prey-capture techniques [6]. Such differentiation can be expected to enhance the carrying capacity (i.e., equilibrium



**Box 3. Implications of personality variation in bluegill sunfish**

Bluegill sunfish (*Lepomis macrochirus*) (Figure 1) are a classic example of personality differences in natural animal populations [46]. Bluegills are freshwater fish that live in the shallow waters of lakes and ponds or in slow-moving areas of streams and small rivers. Until recently, they were considered a generalist predator, adept at feeding in both littoral and open-water habitats. Upon closer inspection, it turned out that there is considerable intraspecific variation in foraging behavior and morphology and that individuals are often foraging specialists rather than generalists. When introduced into a pond, bluegills quickly distribute over habitat types; some individuals consistently stay in the open water, some consistently stay in the littoral zone, and only a few switch between habitats [35]. Differences in microhabitat preference are associated with differences in other behavioral tendencies (e.g., boldness, activity, exploration tendency, learning ability, responsiveness, and diet choice) and morphology (e.g., fin length and body proportions) [35,46,93]. It is conceivable that habitat specialization in bluegills is also related to the well-studied polymorphism in mating strategies in this species [94], although this has apparently not yet been investigated. Under stable environmental conditions, each of the two

habitat specialists achieves a considerably higher foraging success than do habitat generalists [35]. However, specialists are limited in their response to environmental change: specialists for one habitat are often not able to notice and exploit new feeding opportunities occurring in the other habitat [35].

Behavioral differentiation has also considerable consequences for the interaction of bluegills with other species. For example, bluegills specialized on the open-water habitat prevent pumpkinseed sunfish (*Lepomis gibbosus*) from entering this feeding niche [46]. The interaction of sunfish with their prey can strongly depend on both predator and prey personalities, although this has only been studied in species closely related to bluegills [64]. In bluegills, the two habitat specialists encounter different types of predator and parasite, as evidenced by the fact that open-water bluegills have a very different parasite load compared with bluegills living in the littoral [46]. Interestingly, this also applies to human predators because different behavioral types differ substantially in their catchability and human harvesting strategies differentially affect the distribution of behavioral types [95] (Box 4).



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**Figure 1.** Bluegill sunfish in a littoral habitat. Reproduced, with permission, from Eric Engbretson.

population density) and productivity of populations [17]. First, differences in resource and habitat use reduce competition among individuals, resulting in a more extensive and efficient use of resources and habitats and, hence, higher productivity [19,21,35]. Second, different behavioral types might facilitate each other or have other synergistic effects. Western bluebirds (*Sialia mexicana*) [36] provide an example for facilitation; non-aggressive and shy types can only settle in habitats that have been colonized before by aggressive and bold types. Division of labor in group-living species, such as meerkats (*Suricata suricatta*) [37], cooperatively breeding cichlids (*Neolamprologus pulcher*) [38] or eusocial insects [39], exemplify that productivity can be

strongly enhanced by behavioral differentiation. Synergisms can also result from behavioral complementation. For example, breeding oystercatcher pairs (*Haematopus ostralegus*) have higher reproductive success if the male and female are specialized to exploit different types of prey [40].

#### *Implication 3: stability, resilience, and persistence of populations*

Populations harboring different behavioral types can be expected to exhibit less density fluctuation around equilibrium and to be less vulnerable to environmental change [17,41]. First, stochastic fluctuations in the densities of the

various types even out, leading to dampened fluctuations of the population as a whole (averaging effect). Second, different types tend to react differently to environmental change, leading to less extreme responses of variable populations (portfolio effect). Third, when confronted with sudden and drastic environmental changes, more diverse populations are more likely to harbor types that are able to cope with the novel conditions, thus increasing population persistence (insurance effect).

Studies explicitly addressing the relation between behavioral diversity and population stability are still scarce, but the available evidence suggests that variation in behavioral types has a buffering effect at the population level. For example, honey bee colonies with individual differences in fanning behavior maintain more stable brood nest temperatures than do less diverse colonies [42]. Variation in homing behavior of sockeye salmon (*Oncorhynchus nerka*) promotes stock productivity and persistence in the face of changing climatic conditions [29]. Similarly, differences in boldness, habitat and resource use, and competitive ability can be expected to buffer population responses to changing predation pressures, habitat and resource quality, and competitive regimes, respectively.

#### Implication 4: dispersal, colonization, and invasion

Dispersing individuals face different environmental conditions and challenges compared with non-dispersers. Therefore, it is not surprising that dispersal tendency tends to be associated with whole suites of characteristics promoting dispersal success (dispersal syndrome) and settlement success (invasion syndrome). For example, Glanville fritillary butterflies (*Melitaea cinxia*) [43] exhibit heritable variation in dispersal tendency, and these differences are associated with behavioral (locomotor activity and feeding behavior), physiological (metabolic rate), morphological (flight muscle development), and life history (longevity and reproductive rate) variation (see [36] for a similar example).

Within a set of colonizing or invading individuals, differences in behavioral type can be crucial for success, either because of the insurance effect (Implication 3) or because different types are favored at different stages (e.g., transport, introduction, establishment, and spread) of the invasion or colonization process [27]. As a consequence, the mix of behavioral types in a population affects the dynamics, stability, and persistence of a dispersal-connected metapopulation [21,28].

#### Implication 5: distribution within habitats

Personality traits affect not only movements between habitats (Implication 4), but also the distribution of individuals within habitats, leading to a non-random distribution of behavioral types in space and to non-random interactions among behavioral types. For example, in western bluebirds (*Sialia mexicana*) aggressive males establish territories in not only the most profitable, but also the most fiercely competed parts of the habitat, whereas less aggressive males accumulate in less suitable parts of the habitat [44]. Spatial segregation will often enhance the differences between behavioral types with respect to life history, physiology, and morphology (Box 2). It can also be

expected to reduce exploitation competition and enhance interference competition among behavioral types. Moreover, it will have repercussions on trophic interactions and the spread of disease, because it facilitates the (spatial) differentiation of prey, predators, and pathogens. Bluegill sunfish (*Lepomis macrochirus*) provide a good example of many of these effects (Box 3).

Theoretical studies [45] demonstrate that spatial separation can lead to spatial pattern formation and local non-equilibrium dynamics, both of which can have substantial implications for the dynamics and outcome of evolutionary and ecological processes.

#### Implication 6: transmission dynamics: disease and information

Behavioral differentiation can have a large impact on the prevalence and dynamics of infectious diseases and the intensity of their outbreaks. First, behavioral types often differ in their distribution in space (Implication 5), thus exposing them to different infectious agents [46]. Second, behavioral types can differ substantially in the structure and dynamics of their social network, which is a key determinant for the spread of infectious diseases [47,48]. For example, in three-spined sticklebacks (*Gasterosteus aculeatus*), bold individuals tend to have fewer interactions than do shy individuals (i.e., a lower mean strength), but these interactions are more evenly distributed and involve more group members (i.e., a higher mean clustering coefficient) [49]. Third, behavioral types can differ in both their susceptibility to disease and their infectiousness [23]. Models taking account of such individual differences arrive at predictions that differ sharply from average-based approaches [25]. Populations where individuals vary in exposure and susceptibility to infectious agents generally have a lower prevalence of disease and are more buffered against disease-mediated extinction. Variation in contact number, contact rate, and infectiousness, for example, leads to rarer but more explosive outbreaks. This has consequences for disease control (Box 4), where dramatic improvement can be achieved by targeted control policies (e.g., by vaccinating 'superspreaders' [25]).

Similar principles apply to the spread of information in populations [47]. Spatial separation of behavioral types can hamper the availability of information about ecologically relevant events in other habitats [35] (Box 3). The spread of information via social learning depends on the structure of the social network and the ability to acquire and transmit information, which, in turn, are affected by personality traits such as sociability, exploration tendency, boldness, neophilia, and social responsiveness. Moreover, the mix of behavioral types within a group is important for collective decision-making [50] and the use of social information [51]. As in the case of disease, specific individuals of a particular behavioral type often have a key role in the acquisition and spread of information [21,48,52].

#### Implication 7: social evolution

Differences in behavioral type select for social responsiveness [15,53,54]. In turn, the presence of responsive individuals can trigger a coevolutionary process between

**Box 4. Applied issues**

The existence of personality differences in animal populations has implications for a wide range of applied issues [30], including animal breeding and farming (e.g., selection for desirable production traits co-selects for suites of correlated traits, Implication 9); animal welfare (e.g., via differential stress physiology associated with types, Box 1); reintroduction programs and conservation biology (Implications 3, 4 and 8; see also Chapter 9 in [96]); management of invasive species (Implication 4); and disease control (Implication 6). In particular, taking into account the mix of behavioral types present in a population can be crucial (Implications 3 and 8) to predicting how that population will respond to (anthropogenic) environmental changes (e.g., harvesting, climate change, habitat loss or fragmentation, and pollution).

Fisheries provide a good example for the importance of taking personality differences into consideration. Fisheries tend to remove the largest fish, thus indirectly selecting for slow growth and early maturation [97]. However, it has recently been shown that fast-growing behavioral types are more vulnerable to fishing, independent of their body size, because these types are typically also more active, more bold in the face of risks, and more aggressive than their slow-growing conspecifics [97]. This positive coupling between fast growth and vulnerability to fishing suggests that evolutionary changes in harvested fish populations occur more rapidly in populations with differences in personality type. In turn, fast evolutionary responses can affect the ability of populations to recover after a period of harvesting because, once personality variation is depleted, evolution might slow down substantially (Implication 8). This might explain why many fish populations have failed to recover even after long periods with little fishing [98]. Thus, personality differences might give rise to accelerated evolutionary responses in the presence of fishing and retarded responses in the absence of fishing (i.e., recovery). This has obvious implications for policy makers designing rules that aim at sustainable exploitation of fish [99].

responsiveness and the monitored trait that fundamentally changes the direction and outcome of social evolution. First, whenever it is beneficial for social partners to coordinate their actions, the presence of responsive individuals favors high levels of consistency. Several theoretical studies have shown that, starting from ancestral populations with small individual differences, this can result in the evolution of pronounced individual differences in traits such as aggressiveness [53,54], cooperativeness [53,54], and leadership behavior [55]. Second, socially responsive individuals might break up interactions to find new partners. This induces a selection pressure on individuals to exhibit behavior that makes them an attractive partner. For example, small personality differences in cooperativeness can give rise to high levels of cooperation, contrasting very low cooperation in the absence of such differences [15,56,57]. Third, in the presence of responsive individuals, behavior can be used to signal future behavioral intentions. In case of conflicting interests, such signals can only be reliable when they involve costs (handicap principle [58]). This might explain the apparently maladaptive behavior observed in several situations, for example, extremely high levels of aggression in intraspecific interactions [59].

**Implication 8: speed of evolution and adaptive potential**

In the absence of genetic variation, evolution is mutation limited and, thus, potentially very slow. Evolution can be much faster in genetically polymorphic populations,

because the favored alleles might be immediately available [14]. Moreover, the chance that an advantageous allele goes to fixation is higher if it is present in multiple copies, as in the case of polymorphic populations. Thus, when confronted with a new selective regime, populations with genetic differences in behavioral type might be at a substantial advantage over populations without such differences. Differences in behavioral type will often reflect environment-dependent plasticity rather than genetic variation (i.e., a conditional strategy; Box 1). Also in this case, an evolutionary response to environmental change can occur more rapidly than in the absence of such differences because the newly favored phenotypes might already be present in the population. In other words, populations with differences in behavioral type harbor a variety of integrated phenotypes, and such phenotypes do not have to emerge from scratch when environmental conditions change [60–62].

**Implication 9: constraints on adaptive evolution**

As quantified by Lande's multivariate selection equation, the course of adaptive evolution is not only determined by selection differentials, but also by the (additive) genetic variance–covariance matrix quantifying the correlation among traits [63]. Associations among traits can prevent a fitness peak on an adaptive landscape being achieved, or can retard adaptive evolution, given that the associated traits cannot evolve independently. These insights apply directly to personality variation, because behavioral trait correlations are a defining characteristic of personalities (behavioral syndromes; Box 1). Whenever such correlations cannot easily be broken, they can thus constrain the course and outcome of evolution. This might explain seemingly maladaptive behavior associated with behavioral types. For example, streamside salamander larvae (*Ambystoma barbouri*) exhibit positive behavioral correlations of activity levels in the absence and presence of cues from a fish predator: some 'geared up' individuals are consistently more active than other 'geared down' individuals; however, none of these individuals appears to exhibit the optimal behavior under both circumstances (i.e., high activity levels in the absence, and low active levels in the presence, of the fish cues) [64].

**Implication 10: evolvability**

The syndrome structure inherent to personalities might have an important role in promoting the capacity of a population to evolve solutions to novel ecological problems. The trait correlations present in a population with personality differences have been pre-tested in past environments and, thus, should associate traits with each other that, to some extent, also fit to each other well in future environments. Once such trait associations are in place (e.g., by the evolution of regulatory processes), adaptive evolution can proceed in a more efficient way. For example, consider a population that is confronted with a sudden and permanent shift in the temperature regime, raising the temperature to previously unexperienced high levels. Suppose that the new temperature regime requires a coordinated phenotypic shift in a whole suite of behavioral and physiological traits (e.g., metabolic rate, activity level, timing of



reproduction, foraging and breeding behavior). Whether this new phenotype can evolve, and how long that takes, will crucially depend on the existence of a syndrome. If a variety of traits have to evolve independently, the waiting time for the right set of correlated mutations can be extremely long [14,65]. If, by contrast, traits are associated in syndromes (e.g., as a response to slight temperature fluctuations in the ancestral environment), traits already co-vary in a systematic way (e.g., due to joint regulation). As a consequence, the high-dimensional trait space collapses into a lower-dimensional space of regulatory parameters, where adaptive evolution occurs faster by orders of magnitude [65,66].

#### *Implication 11: eco-evolutionary dynamics*

When evolutionary responses to ecological change occur sufficiently rapidly, ecological and evolutionary dynamics proceed at similar timescales. In such cases, evolution can have a substantial impact, both quantitatively and qualitatively, on the course and outcome of population dynamics, the dynamics of communities, and even of whole ecosystems [22,67]. Up to now, research on eco-evolutionary dynamics has largely neglected differences in behavioral type. In view of the fact that such differences can speed up adaptive evolution considerably (Implication 8), this is surprising. Moreover, there are several examples of the interplay of population dynamics and the evolution of behavioral syndromes. Several studies show that the interaction of population increase and selection on aggressiveness and dispersal contributes to the population cycles of voles and other mammals in northern Canada [68,69], as well as to the metapopulation dynamics of western bluebirds [36] and Glanville fritillary butterflies [70] (Implications 4 and 5). The evolution of mating strategies is often characterized by a rapid turnover [71] that can have strong effects on ecological factors such as density regulation and demographic stochasticity [72]. Finally, the rapid coevolution of predators and prey, or hosts and their parasites, is often mediated by behavior [73]. We consider it probable that differences in behavioral type (in particular in those cases where they are maintained by non-equilibrium dynamics [10]) will have an important role when ecology and evolution occur on similar timescales.

#### *Implication 12: speciation*

Behavior has an important role in speciation [74], and there are various arguments suggesting a link between differentiation into behavioral types and speciation. In the classic allopatric scenario, speciation is initiated by geographical isolation, followed by the differentiation of the separate subspecies. The relevance of this scenario for speciation depends on the speed of differentiation in relation to the duration of the barrier to gene flow. Differences in behavioral type can strongly enhance the speed of directional evolution and adaptation to local conditions (Implication 8), thereby contributing to the rapid divergence of incipient species. Speciation is often initiated if parts of a population enter a new habitat or adopt a new lifestyle [75] and behavioral syndromes can increase the likelihood of settling successfully in a new habitat

(Implication 4). Therefore, one would predict that speciation rates are higher in the presence of such syndromes.

In the presence of substantial gene flow, speciation can unfold if incipient species are driven apart by strong disruptive selection [76,77]. Such 'competitive speciation' is most probable when the spectrum of exploitable resources is broad and each organism is constrained to being a resource specialist [77]. Personality differences can contribute to both aspects; a broad resource spectrum (i.e., a more variable prey species) and resource specialization. However, behavioral types can also hamper competitive speciation, because disruptive selection will often be weakened in the presence of individual variation [78]. The evolution of reproductive isolation is perhaps the crucial step to achieve speciation in the presence of gene flow. This process is strongly facilitated by the presence of 'magic traits', that is, traits that are both subject to divergent selection and contribute to non-random mating [79]. The correlation structure inherent to personalities can correspond to a magic trait, if the syndrome includes traits that are of ecological relevance as well as of relevance for mating.

#### *Implication 13: species interactions*

The distribution of behavioral types in one species constitutes part of the ecological and selective environment of other species, thus affecting the ecological interaction dynamics as well as the coevolution of species. For example, individual differences in competitive ability can foster the coexistence of species that would otherwise competitively exclude each other [80]. Variation in food specialization on the side of the predator can have major effects on the dynamics and outcome of predator–prey interactions (e.g., alternative stable states, ecological transients of exclusion or facilitation, and chaos) [81]. The presence of behavioral variation can lead to interesting patterns of coadaptation and a close interplay between ecological and (co-)evolutionary dynamics [82].

On a larger scale, differences in behavioral type can affect the structure and dynamics of species interaction networks [83]. Different types will differ in the parasites, predators, and prey they interact with. Species harboring multiple behavioral types will tend to interact with more species, and the strength of species interactions will often be weaker and/or more diverse [17,21]. Both increased network connectivity and decreased interaction strengths tend to promote network stability and persistence [17,84]. Depending on the size of the species network, variation in interaction strength can have either a stabilizing or a destabilizing effect on interaction networks [84].

#### *Implication 14: community structure and ecosystem processes*

Recent work in community genetics has revealed that genetic variation in primary producers can have cascading effects on community dynamics, community structure, and ecosystem processes [85]. Recent studies suggest that variation in behavioral types can have similar effects. For example, differences in life history and foraging morphology among populations of alewives (*Alosa pseudoharengus*)

give rise to differences in zooplankton community structure, zooplankton biomass, and the strength of trophic cascades [86]. Populations of Trinidadian guppies (*Poecilia reticulata*), characterized by differences in diet use, cause the divergence of ecosystem structure (algal, invertebrate, and detrital standing stocks) and function (gross primary productivity, leaf decomposition rates, and nutrient flux) [87]. The mesocosm experiments of Harmon and colleagues [88] with three-spined sticklebacks are particularly revealing. When compared with a single generalist, mixed populations of food and habitat specialists had largely differing effects on total primary production, prey community structure, and the underwater light regime.

## Conclusions

We have provided an inventory of the consequences of personality differences. The emerging picture is clear: personality differences can be expected to have substantial consequences for key ecological and evolutionary processes, and the interaction of both (Table 1). This is in line with a surge of recent work pointing to the importance of intraspecific variation for ecological and evolutionary processes [14–22]. At present, most of this work focuses on genetic differences or differences in resource use (but see [15,21]). Our review shows that personality differences are an important third dimension of ecologically and evolutionary relevant intraspecific variation.

Personality differences matter. First, personality differences refer to variation that is highly structured both over time and across different situations and contexts. We have seen that precisely this structure can trigger ecological and evolutionary consequences that would not be expected in the presence of less structured variation [see our discussions of the pace-of-life syndrome (Implication 1), social evolution (Implication 7), evolvability (Implication 10), and magic traits in the context of speciation (Implication 12)]. Second, several personality traits are linked to movement in space and we have seen that the resulting non-random distribution and interaction structure of phenotypes can have substantial ecological and evolutionary consequences (Implication 5, but also Implications 2, 4, and 6). Third, personality differences promote the emergence of all kinds of other ecologically and evolutionarily relevant differences (Box 2), for example, life-history differences (Implication 1), physiological and neurobiological differences, and differences in the spread of information and disease (Implication 6). Fourth, personality differences are an important, yet up to now largely neglected, dimension of biodiversity, affecting the stability, resilience, and persistence of populations, communities, and whole ecosystems both at ecological (Implication 3) and evolutionary (Implications 8 and 10) timescales.

We are aware of the fact that several of the above implications are based on plausibility arguments and suggestive case studies rather than on firm evidence. In our opinion, this does not invalidate our arguments. Instead, it reflects the fact that, until recently, within-population differences in behavioral type were largely neglected by ecologists, whereas the potential role of such differences as an important driver of ecological and evolutionary change was insufficiently appreciated by theoreticians

and empirical biologists alike. What is needed now is the development of models translating verbal arguments on the consequences of personality differences into clear-cut (quantitative) predictions, and empirical research to test these predictions.

## Acknowledgments

We thank Dan Blumstein and Paul Craze as well as two anonymous reviewers for constructive criticism and valuable comments.

## References

- 1 Reale, D. *et al.* (2010) Evolutionary and ecological approaches to the study of personality. *Philos. Trans. R. Soc. B* 365, 3937–3946
- 2 Sih, A. *et al.* (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19, 372–378
- 3 Bell, A.M. *et al.* (2009) The repeatability of behaviour: a meta-analysis. *Anim. Behav.* 77, 771–783
- 4 Gosling, S.D. (2001) From mice to men: what can we learn about personality from animal research? *Psychol. Bull.* 127, 45–86
- 5 Reale, D. *et al.* (2007) Integrating animal temperament within ecology and evolution. *Biol. Rev.* 82, 291–318
- 6 Sih, A. *et al.* (2004) Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* 79, 241–277
- 7 Biro, P.A. and Stamps, J.A. (2010) Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends Ecol. Evol.* 25, 653–659
- 8 Dingemanse, N.J. and Wolf, M. (2010) Recent models for adaptive personality differences: a review. *Philos. Trans. R. Soc. B* 365, 3947–3958
- 9 Sih, A. and Bell, A.M. (2008) Insights for behavioral ecology from behavioral syndromes. *Adv. Study Behav.* 38, 227–281
- 10 Wolf, M. and Weissing, F.J. (2010) An explanatory framework for adaptive personality differences. *Philos. Trans. R. Soc. B* 365, 3959–3968
- 11 Biro, P.A. and Stamps, J.A. (2008) Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* 23, 361–368
- 12 Wolf, M. *et al.* (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* 447, 581–584
- 13 Bergmüller, R. and Taborsky, M. (2010) Animal personality due to social niche specialisation. *Trends Ecol. Evol.* 25, 504–511
- 14 Barrett, R.D.H. and Schluter, D. (2008) Adaptation from standing genetic variation. *Trends Ecol. Evol.* 23, 38–44
- 15 McNamara, J.M. and Leimar, O. (2010) Variation and the response to variation as a basis for successful cooperation. *Philos. Trans. R. Soc. B* 365, 2627–2633
- 16 Whitham, T.G. *et al.* (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* 7, 510–523
- 17 Bolnick, D.I. *et al.* (2011) Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26, 183–192
- 18 Bolnick, D.I. *et al.* (2003) The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* 161, 1–28
- 19 Hughes, A.R. *et al.* (2008) Ecological consequences of genetic diversity. *Ecol. Lett.* 11, 609–623
- 20 Violle, C. *et al.* (2012) The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* 27, 244–252
- 21 Sih, A. *et al.* (2012) Ecological implications of behavioural syndromes. *Ecol. Lett.* 15, 278–289
- 22 Pelletier, F. *et al.* (2009) Eco-evolutionary dynamics. *Philos. Trans. R. Soc. B* 364, 1483–1489
- 23 Barber, I. and Dingemanse, N.J. (2010) Parasitism and the evolutionary ecology of animal personality. *Philos. Trans. R. Soc. B* 365, 4077–4088
- 24 Kortet, R. *et al.* (2010) Parasitism, predation and the evolution of animal personalities. *Ecol. Lett.* 13, 1449–1458
- 25 Lloyd-Smith, J.O. *et al.* (2005) Superspreading and the effect of individual variation on disease emergence. *Nature* 438, 355–359
- 26 Chapple, D.G. *et al.* (2012) Can behavioral and personality traits influence the success of unintentional species introductions? *Trends Ecol. Evol.* 27, 57–64
- 27 Fogarty, S. *et al.* (2011) Social personality polymorphism and the spread of invasive species: a model. *Am. Nat.* 177, 273–287



- 28 Cote, J. *et al.* (2010) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philos. Trans. R. Soc. B* 365, 4065–4076
- 29 Schindler, D.E. *et al.* (2010) Population diversity and the portfolio effect in an exploited species. *Nature* 465, 609–612
- 30 Conrad, J.L. *et al.* (2011) Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *J. Fish Biol.* 78, 395–435
- 31 Reale, D. *et al.* (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos. Trans. R. Soc. B* 365, 4051–4063
- 32 Smith, B.R. and Blumstein, D.T. (2008) Fitness consequences of personality: a meta-analysis. *Behav. Ecol.* 19, 448–455
- 33 Wolf, M. and McNamara, J.M. (2012) On the evolution of personalities via frequency-dependent selection. *Am. Nat.* 179, 679–692
- 34 Roff, D.A. (ed.) (2002) *Life History Evolution*, Sinauer Associates
- 35 Werner, E.E. *et al.* (1981) The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology* 62, 116–125
- 36 Duckworth, R.A. (2008) Adaptive dispersal strategies and the dynamics of a range expansion. *Am. Nat.* 172, S4–S17
- 37 Clutton-Brock, T.H. *et al.* (2004) Behavioural tactics of breeders in cooperative meerkats. *Anim. Behav.* 68, 1029–1040
- 38 Le Vin, A.L. *et al.* (2011) Individual variation in helping in a cooperative breeder: relatedness versus behavioural type. *Anim. Behav.* 82, 467–477
- 39 Duarte, A. *et al.* (2011) An evolutionary perspective on self-organized division of labor in social insects. *Annu. Rev. Ecol. Syst.* 42, 91–110
- 40 Van de Pol, M. *et al.* (2010) Fluctuating selection and the maintenance of individual and sex-specific diet specialization in free-living oystercatchers. *Evolution* 64, 836–851
- 41 McCann, K.S. (2000) The diversity–stability debate. *Nature* 405, 228–233
- 42 Oldroyd, B.P. and Fewell, J.H. (2007) Genetic diversity promotes homeostasis in insect colonies. *Trends Ecol. Evol.* 22, 408–413
- 43 Saastamoinen, M. *et al.* (2009) Significant effects of Pgi genotype and body reserves on lifespan in the Glanville fritillary butterfly. *Proc. R. Soc. B* 276, 1313–1322
- 44 Duckworth, R.A. (2006) Aggressive behaviour affects selection on morphology by influencing settlement patterns in a passerine bird. *Proc. R. Soc. B* 273, 1789–1795
- 45 Nowak, M.A. *et al.* (2010) Evolutionary dynamics in structured populations. *Philos. Trans. R. Soc. B* 365, 19–30
- 46 Wilson, D.S. (1998) Adaptive individual differences within single populations. *Philos. Trans. R. Soc. B* 353, 199–205
- 47 Krause, J. *et al.* (2007) Social network theory in the behavioural sciences: potential applications. *Behav. Ecol. Sociobiol.* 62, 15–27
- 48 Krause, J. *et al.* (2010) Personality in the context of social networks. *Philos. Trans. R. Soc. B* 365, 4099–4106
- 49 Pike, T.W. *et al.* (2008) Behavioural phenotype affects social interactions in an animal network. *Proc. R. Soc. B* 275, 2515–2520
- 50 Michelena, P. *et al.* (2010) Personality and collective decision-making in foraging herbivores. *Proc. R. Soc. B* 277, 1093–1099
- 51 Kurvers, R. *et al.* (2010) Personality predicts the use of social information. *Ecol. Lett.* 13, 829–837
- 52 Sih, A. *et al.* (2009) Social network theory: new insights and issues for behavioral ecologists. *Behav. Ecol. Sociobiol.* 63, 975–988
- 53 Dall, S.R.X. *et al.* (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* 7, 734–739
- 54 Wolf, M. *et al.* (2011) On the coevolution of social responsiveness and behavioural consistency. *Proc. R. Soc. B* 278, 440–448
- 55 Johnstone, R.A. and Manica, A. (2011) Evolution of personality differences in leadership. *Proc. Natl. Acad. Sci. U.S.A.* 108, 8373–8378
- 56 McNamara, J.M. *et al.* (2008) The coevolution of choosiness and cooperation. *Nature* 451, 189–192
- 57 McNamara, J.M. *et al.* (2004) Variation in behaviour promotes cooperation in the Prisoner's Dilemma game. *Nature* 428, 745–748
- 58 Zahavi, A. *et al.*, eds (1999) *The Handicap Principle: A Missing Piece of Darwin's Puzzle*, Oxford University Press
- 59 Koolhaas, J.M. *et al.* (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* 23, 925–935
- 60 Wolf, M. *et al.* (2008) Do animal personalities emerge? Reply. *Nature* 451, E9–E10
- 61 Pfennig, D.W. *et al.* (2010) Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol. Evol.* 25, 459–467
- 62 West-Eberhard, M.J. (ed.) (2003) *Developmental Plasticity and Evolution*, Oxford University Press
- 63 Arnold, S.J. (1992) Constraints on phenotypic evolution. *Am. Nat.* 140, S85–S107
- 64 Sih, A. *et al.* (2003) Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Anim. Behav.* 65, 29–44
- 65 Wagner, G.P. and Altenberg, L. (1996) Perspective: complex adaptations and the evolution of evolvability. *Evolution* 50, 967–976
- 66 Wagner, A. (ed.) (2005) *Robustness and Evolvability in Living Systems*, Princeton University Press
- 67 Ellner, S.P. *et al.* (2011) Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecol. Lett.* 14, 603–614
- 68 Krebs, C.J. (2011) Of lemmings and snowshoe hares: the ecology of northern Canada. *Proc. R. Soc. B* 278, 481–489
- 69 Myers, J.H. and Krebs, C.J. (1971) Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecol. Monogr.* 41, 53–78
- 70 Hanski, I. and Mononen, T. (2011) Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. *Ecol. Lett.* 14, 1025–1034
- 71 van Doorn, G.S. and Weissing, F.J. (2006) Sexual conflict and the evolution of female preferences for indicators of male quality. *Am. Nat.* 168, 742–757
- 72 Sinervo, B. (2001) Runaway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. *Genetica* 112, 417–434
- 73 Palkovacs, E.P. *et al.* (2009) Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philos. Trans. R. Soc. B* 364, 1617–1628
- 74 Duckworth, R.A. (2009) The role of behavior in evolution: a search for mechanism. *Evol. Ecol.* 23, 513–531
- 75 Nyman, T. (2010) To speciate, or not to speciate? Resource heterogeneity, the subjectivity of similarity, and the macroevolutionary consequences of niche-width shifts in plant-feeding insects. *Biol. Rev.* 85, 393–411
- 76 Weissing, F.J. *et al.* (2011) Adaptive speciation theory: a conceptual review. *Behav. Ecol. Sociobiol.* 65, 461–480
- 77 Dieckmann, U. and Doebeli, M. (1999) On the origin of species by sympatric speciation. *Nature* 400, 354–357
- 78 Rueffler, C. *et al.* (2006) Disruptive selection and then what? *Trends Ecol. Evol.* 21, 238–245
- 79 Servedio, M.R. *et al.* (2011) Magic traits in speciation: 'magic' but not rare? *Trends Ecol. Evol.* 26, 389–397
- 80 Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343–366
- 81 Schreiber, S.J. *et al.* (2011) The community effects of phenotypic and genetic variation within a predator population. *Ecology* 92, 1582–1593
- 82 Nakajima, M. *et al.* (2004) Persistence and fluctuation of lateral dimorphism in fishes. *Am. Nat.* 163, 692–698
- 83 Moya-Larano, J. (2011) Genetic variation, predator–prey interactions and food web structure. *Philos. Trans. R. Soc. B* 366, 1425–1437
- 84 Gross, T. *et al.* (2009) Generalized models reveal stabilizing factors in food webs. *Science* 325, 747–750
- 85 Rowntree, J.K. *et al.* (2011) Forward from the crossroads of ecology and evolution. *Philos. Trans. R. Soc. B* 366, 1322–1328
- 86 Post, D.M. *et al.* (2008) Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology* 89, 2019–2032
- 87 Bassar, R.D. *et al.* (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proc. Natl. Acad. Sci. U.S.A.* 107, 3616–3621
- 88 Harmon, L.J. *et al.* (2009) Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458, 1167–1170
- 89 Careau, V. *et al.* (2008) Energy metabolism and animal personality. *Oikos* 117, 641–653
- 90 Reddon, A.R. and Hurd, P.L. (2009) Individual differences in cerebral lateralization are associated with shy–bold variation in the convict cichlid. *Anim. Behav.* 77, 189–193

- 91 van Oers, K. *et al.* (2005) Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour* 142, 1185–1206
- 92 Weislo, W.T. (1989) Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Syst.* 20, 137–169
- 93 Wilson, A.D.M. and Godin, J.G.J. (2009) Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behav. Ecol.* 20, 231–237
- 94 Neff, B.D. *et al.* (2003) Sperm investment and alternative mating tactics in bluegill sunfish (*Lepomis macrochirus*). *Behav. Ecol.* 14, 634–641
- 95 Wilson, A.D.M. *et al.* (2011) Capture technique and fish personality: angling targets timid bluegill sunfish, *Lepomis macrochirus*. *Can. J. Fish. Aquat. Sci.* 68, 749–757
- 96 Blumstein, D.T. and Fernández-Juricic, E., eds (2010) *A Primer of Conservation Behavior*, Sinauer Associates
- 97 Biro, P.A. and Post, J.R. (2008) Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proc. Natl. Acad. Sci. U.S.A.* 105, 2919–2922
- 98 Hutchings, J.A. and Reynolds, J.D. (2004) Marine fish population collapses: consequences for recovery and extinction risk. *Bioscience* 54, 297–309
- 99 Jørgensen, C. *et al.* (2007) Ecology – managing evolving fish stocks. *Science* 318, 1247–1248
- 100 Kobler, A. *et al.* (2009) Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia* 161, 837–847