

Behavioral syndromes: an ecological and evolutionary overview

Andrew Sih¹, Alison Bell² and J. Chadwick Johnson³

¹Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

²Department of Environmental and Evolutionary Biology, Graham Kerr Building, University of Glasgow, UK, G12 8QQ

³Division of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Toronto, Ontario, Canada, M1C 1A4

Recent studies suggest that populations and species often exhibit behavioral syndromes; that is, suites of correlated behaviors across situations. An example is an aggression syndrome where some individuals are more aggressive, whereas others are less aggressive across a range of situations and contexts. The existence of behavioral syndromes focuses the attention of behavioral ecologists on limited (less than optimal) behavioral plasticity and behavioral carryovers across situations, rather than on optimal plasticity in each isolated situation. Behavioral syndromes can explain behaviors that appear strikingly non-adaptive in an isolated context (e.g. inappropriately high activity when predators are present, or excessive sexual cannibalism). Behavioral syndromes can also help to explain the maintenance of individual variation in behavioral types, a phenomenon that is ubiquitous, but often ignored. Recent studies suggest that the behavioral type of an individual, population or species can have important ecological and evolutionary implications, including major effects on species distributions, on the relative tendencies of species to be invasive or to respond well to environmental change, and on speciation rates. Although most studies of behavioral syndromes to date have focused on a few organisms, mainly in the laboratory, further work on other species, particularly in the field, should yield numerous new insights.

Humans show consistent individual differences in personality [1]. For example, some people are generally more bold, whereas others are generally more shy. In statistical terms, the tendency for individuals to differ consistently in behavior (e.g. in boldness) across SITUATIONS (see Glossary) is quantified as a BEHAVIORAL CORRELATION ACROSS SITUATIONS. The analog of personality has been studied in considerable detail in a few primates, domesticated animals and laboratory rodents [2,3], with much of the focus being on the genetic and neuroendocrine bases of variation in BEHAVIORAL TYPE. However, recent studies by ethologists and behavioral ecologists have documented 'animal personalities' in a broad range of 'non-model organisms', including several mammals, birds, lizards, amphibians, fish, mollusks and arthropods [3]. Evolutionary ecologists refer to suites of correlated traits as syndromes;

for example, life-history or dispersal syndromes [4,5]. We therefore refer to suites of correlated behaviors as BEHAVIORAL SYNDROMES. A population or species can exhibit a behavioral syndrome with each individual showing a behavioral type (e.g. more bold or more shy). Alternatively, a group of species can exhibit a syndrome with each species having a behavioral type (e.g. species that are more bold versus those that are more shy).

The idea of studying correlated suites of behaviors across situations represents an important shift in how behavioral ecologists typically address behavior [6]. In essence, when traits are correlated, they should be studied together, as a package, rather than as isolated units. Here, we describe why behavioral syndromes should be important and we review recent studies that show that behavioral syndromes have major effects on individual fitness, species distributions (including species invasions) and speciation rates. We also identify crucial directions for future empirical and theoretical work.

Why are behavioral syndromes important?

Consider an aggression syndrome where some individuals are more aggressive than others across a range of situations. All individuals shift their aggression levels up or down depending on the situation; however, some remain consistently more aggressive than others (i.e. their rank order is maintained). More aggressive individuals should do well in competitive situations where aggression is favored; however, if the general aggressive tendency

Glossary

Behavioral correlation across situations: between-individual consistency across situations that can either involve the same context but in different situations (e.g. feeding activity in the presence versus absence of predators), or different contexts in different situations (e.g. aggression towards conspecifics in the absence of predators versus feeding activity in the presence of predators).

Behavioral syndrome: a suite of correlated behaviors reflecting between-individual consistency in behavior across multiple (two or more) situations. A population or species can exhibit a behavioral syndrome. Within the syndrome, individuals have a **behavioral type** (e.g. more aggressive versus less aggressive behavioral types).

Context: a functional behavioral category; e.g. feeding, mating, antipredator, parental care, contest or dispersal contexts.

Situation: a given set of conditions at one point in time. Different situations could involve different levels along an environmental gradient (e.g. different levels of predation risk) or different sets of conditions across time (e.g. the breeding season versus the non-breeding season).

carries over into other situations, aggressive individuals might be unsuitably aggressive in CONTEXTS where caution or care are more appropriate (e.g. in an antipredator or parental care context). Conversely, less aggressive individuals might do well in situations where low aggression is favored, but poorly in competitive situations.

This simple notion shifts classic thinking in behavioral ecology in several ways [6]. First, whereas behavioral ecologists typically treat behavior as being potentially infinitely plastic (all individuals can exhibit the optimal behavior in all contexts), the notion of behavioral syndromes implies limited behavioral plasticity. The very idea that we can classify individuals as being more versus less aggressive implies a limit to their range of plasticity. Second, whereas behavioral ecologists tend to study ecological situations (e.g. behavior during mating versus non-mating seasons) in isolation from each other, the behavioral syndrome idea suggests the need to track individual behavior and performance across situations (i.e. to study aspects of an overall syndrome in an integrated fashion). For example, to understand individual variation in parental care behavior fully, it might be necessary to study how it is correlated with contest behavior, or antipredator behavior, and vice versa. The existence of limited plasticity and behavioral correlations can cause individuals to often exhibit behavior that appears suboptimal when viewed in isolation. Finally, whereas behavioral ecology often ignores individual variation in behavior (focusing instead on shifts in average behavior in response to environmental variation [7,8]), the behavioral syndrome framework quantifies individual variation in behavior and attempts to explain the maintenance of this variation.

Types of ecologically important behavioral syndromes

Tradeoffs play a crucial role in explaining many ecological and evolutionary patterns. Therefore, behavioral syndromes should be particularly important when they generate tradeoffs or conflicts. In predator–prey ecology, a fundamental tradeoff centers on activity. For prey, the standard view about this tradeoff involves a within-situation time budget conflict [9] where, when predators are present, increased prey activity results in higher prey feeding rates, but also higher predation risk [10–12]. The behavioral syndrome view posits the existence of an across-situation conflict that occurs if activity levels are positively correlated across situations, such as with versus without predators. Individuals that are more active than others in the absence of predators (and thus feed and grow at higher rates) might be inappropriately active in the presence of predators (and thus suffer high predation rates). Interestingly, although many experimental studies have documented how average prey activity levels (or refuge use) differ in the presence versus absence of predators, few studies have looked at activity correlations across situations. An example of the latter involves streamside salamander prey, *Ambystoma barbouri*, which exhibited positive phenotypic and genetic (using full-sib analyses) correlations between activity (or time out of refuge) in the presence versus absence of cues from

predatory sunfish *Lepomis cyanellus* [9]. Separate studies found that activity of *A. barbouri* in the absence of predators is correlated to growth rates [13] and that activity results in high sunfish predation [14]. Brodin and Johansson [15] found parallel results in the damselfly *Coenagrion hastulatum*.

Another ecologically important behavioral axis is aggressiveness, or the tendency to attack other individuals. For example, more aggressive funnel web spiders *Agelenopsis aperta* are quicker to attack both prey and conspecific territorial intruders than are less aggressive spiders [16]. Subsequent work showed that aggressive spiders also exhibit higher levels of non-adaptive wasteful killing, where spiders kill but then do not consume prey [17]. A particularly intriguing consequence of this syndrome is a spillover to sexual cannibalism (where females attack and consume courting males). Arnqvist and Henriksson [18] documented non-adaptive, excess pre-copulatory sexual cannibalism in a fishing spider where some females apparently attack every male that they encounter and thus do not mate. The authors hypothesized that this behavior could be explained as a non-adaptive carryover from a general feeding aggression syndrome; that is, strong selection favoring high feeding voracity in juvenile females (owing to strong food limitation) might spillover to cause an inappropriately high tendency for those females (when they mature to adulthood) to attack males.

Several studies have found that aggressiveness is correlated to boldness. One of the first studies to document correlations between behaviors in different contexts showed that individual male stickleback *Gasterosteus aculeatus* hypothesized that this correlation might reflect the shared effects of gonadal steroids on both behaviors [19]. Riechert and Hedrick [16] also found that more aggressive female spiders were more bold (quicker to emerge from hiding after a simulated attack). The existence of a general aggressive–bold syndrome means that the evolution of feeding, mating, territorial and antipredator behavior might be best studied together, rather than as independent activities.

Boldness *per se* has also been the focus of study [20–22]. Bold sunfish *Lepomis gibbosus* acclimate more quickly to the laboratory, feed more on exposed, difficult to capture prey, and engage in more predator inspection than do shy sunfish. Not only do bold and shy individuals differ in a variety of behaviors, they also differ in the types of parasite that they carry. This is presumably because they use different habitats as a result of their behavioral type, thus exposing them to different parasite species [21]. Studies of other organisms found that, relative to shy individuals, bold male guppies are more attractive to females [23], bold killifish and bold great tits *Parus major* disperse further in the field [24,25], and bold bighorn sheep have higher weaning success and better survival in the field [26,27].

Finally, a behavioral syndrome that has only recently received attention from behavioral ecologists is the proactive–reactive axis [2,27]. Proactive individuals are both aggressive and bold. They actively explore their environment, manipulate environmental challenges and readily form persistent routines. By contrast, reactive

individuals pay careful attention to external stimuli, adjusting cautiously to changes in the environment. These different ‘coping styles’ are thought to represent alternative, coherent, adaptive strategies [2]. Whereas proactive individuals tend to dominate and outcompete reactive ones in a stable environment, reactive individuals appear to respond better to changing environments. This syndrome has been documented in laboratory rodents [28,29], pigs [30], captive mink [31] and chickens [32], with most previous work focusing on genetic and neuroendocrine correlates of these different coping styles.

Perhaps the most complete study of the ecological and evolutionary significance of a behavioral syndrome involves work with great tits. Initial work found consistent individual differences in exploratory behavior (activity in an unfamiliar environment). Relative to ‘slow’ explorers, ‘fast’ explorers were also more aggressive [33], less neophobic [34] and more likely to form routines [33,34]. Artificial selection over four generations produced fast, bold, proactive versus slow, shy, reactive birds, thus demonstrating that exploratory behavior and coping styles are heritable [35–37]. ‘Slow’ and ‘fast’ lines also differed in hormone profiles [38] and responses to social defeat [39]. Field studies estimated the heritability of exploratory behavior in the wild [40], and quantified the fitness consequences of the different behavioral strategies in nature [41]. Notably, selection on the two strategies depended on the intensity of competition (which fluctuated between years, and differed between the sexes). Fast explorers had higher fitness when competition was intense, whereas slow explorers did better when competition was relaxed. Temporal variation in competitive regimes might help explain the maintenance of the two strategies in the population.

How broad and stable are behavioral syndromes?

All else being equal, behavioral syndromes should be particularly important if they extend across a broad range of contexts (or what psychologists call ‘domains’). For example, a broad syndrome might involve correlations among feeding, mating, contest, antipredator, parental care and dispersal behaviors. Alternatively, syndromes can be domain specific [21]; that is, behaviors might be correlated within one specific domain (e.g. within the mating domain, aggression towards males and females might be correlated), but decoupled across different domains (e.g. aggression in the mating domain might be unrelated to aggression in feeding or antipredator domains). Empirical tests of this issue have yielded mixed results. Whereas some studies have documented significant correlations across domains [28–32,37], others have revealed domain-specific correlations [21,26,42]. More studies are needed to discern generalities on the breadth of behavioral syndromes (i.e. on the range of behavioral correlations).

Similarly, syndromes should be particularly important if they are stable over long periods during the life of an organism. One obvious aspect involves the stability of the behavioral type of each individual. Do more aggressive individuals remain more aggressive than others over a lifetime? A subtly different issue is the stability of the

syndrome itself. Is the suite of correlations maintained over ontogeny, or is the syndrome decoupled at some point in the life cycle? Although these issues have been studied in humans [43], they have only recently begun to receive attention from animal behaviorists (e.g. A.M. Bell, PhD thesis, University of California at Davis, 2003; C. Carere, PhD thesis, University of Groningen, 2003).

Evolution and behavioral syndromes

Explicit evolutionary theory has not yet been developed for behavioral syndromes; however, some insights can be drawn from parallels with existing, related evolutionary theory (Boxes 1,2). Two key interrelated aspects of behavioral syndromes are limited behavioral plasticity and behavioral correlations across situations. From an unconstrained optimality view, animals should show optimal plasticity, and selection should decouple correlations that cause conflicts. Yet these constraints appear to sometimes persist. Why? Models of the evolution of

Box 1. Behavioral syndromes and adaptive phenotypic plasticity

Phenotypic plasticity is ‘the change in the expressed phenotype of a genotype as a function of the environment’ [62]. Although this definition includes behavioral plasticity, the literature on phenotypic plasticity focuses on induced changes in morphology, physiology or life histories [63], rather than on behavior. Behavioral ecologists often wonder why behavior is excluded from phenotypic plasticity [64]. In fact, there are key conceptual differences between developmental plasticity, the main focus of the study of phenotypic plasticity, and behavior, that justify why the two should be analyzed by different approaches. Behavioral ecology usually assumes that behavioral plasticity is unlimited (individuals can always exhibit the optimum), immediate (little or no time lag) and infinitely reversible. By contrast, developmental plasticity is often thought to unfold slowly, and be irreversible [50,65]. Behavioral syndromes fall between these two extremes, perhaps closer to developmental plasticity. Once the behavioral type of an individual is set by a combination of its genotype and developmental environment (Box 3), it exhibits limited behavioral plasticity and it might take time to shift its behavior.

Theory about the evolution of adaptive phenotypic plasticity based on reaction norms [50,65,66] can thus provide preliminary insights into the evolution of behavioral syndromes. For example, models of phenotypic plasticity can explain when and why natural selection favors limited plasticity. The key assumption is that, because plasticity is either irreversible or reversible but with time lags [66], in an unpredictably varying environment, plastic individuals risk spending some time with the wrong phenotype. If prey grow a spine as an antipredator trait, they can be stuck with it (even if it reduces feeding efficiency), or it can take a long time to lose it even after predators leave. Given unavoidable errors, it can be better to be less plastic [65,66]. Low plasticity can also be favored if there are large costs of plasticity (e.g. costs of gathering information required to make decisions [44,67]).

Theory about phenotypic plasticity also yields predictions about factors that should affect the expected mean phenotype in a variable environment [50,65,66]. All else being equal, the optimal reaction norm should be more heavily influenced by selection in: (i) environments that individuals experience more frequently; (ii) environments with stronger selection *per se* (i.e. a stronger effect of the focal phenotype on fitness); and (iii) higher quality environments (i.e. sources versus sinks, [68]). These predictions seem reasonable for behavioral syndromes; however, theory devised explicitly to address behavioral syndromes is needed to explore these ideas further.

Box 2. Behavioral syndromes as evolutionary constraints

Quantitative geneticists have long suggested that genetic correlations between traits can act as evolutionary constraints [69]. That is, if two traits are genetically correlated, then selection on one can produce an indirect, correlated response in the other. If the correlated response is deleterious, a focal trait can be prevented from reaching its optimal value. Genetic correlations between morphological traits are well documented, and correlated responses to artificial and natural selection on morphological traits have often been reported [69].

Genetic correlations, however, are not necessarily set; they can evolve. For example, artificial selection experiments with very small components of the *Drosophila* wing suggest that even tightly integrated allometric relationships can be dissociated [70]. Given that genetic correlations can themselves evolve, some argue that selection should favor the evolution of adaptive genetic correlations between traits [71–73]. For example, if pleiotropy (where one gene controls two or more traits) causes a maladaptive behavioral correlation, then selection should favor genetic modifiers that alter the pleiotropy to decouple the correlation. Overall, natural selection should produce adaptive phenotypes with functionally integrated suites of traits (71–73).

The ‘constraint’ versus ‘adaptive’ views of genetic correlations make different predictions about how correlations between behavioral traits might differ from one environment to another, or about the evolutionary stability of behavioral syndromes. If genetic correlations between behaviors act as constraints, then behavioral syndromes should be difficult to break apart. If, for example, aggression and boldness are positively correlated (the same individuals are both more aggressive and more bold than other individuals) in one population, they should also be positively correlated in other populations of the same species. Furthermore, behavioral correlations among populations should be in the same direction as the correlations within populations. Populations that are, on average, more bold than other populations, should also be more aggressive. By contrast, in the ‘adaptive’ view, correlations between a given pair of behaviors might vary substantially if different correlations are favored in different environments. Only a few studies, to date, have addressed population variation in behavioral correlations [74,75]. One study found differences between populations of sticklebacks *Gasterosteus aculeatus* in behavioral correlations, and different relationships between aggression and boldness within versus between populations (A.M. Bell, PhD thesis, University of California, Davis, 2003). Both of these patterns support the ‘adaptive view’ of behavioral correlations.

phenotypic plasticity can explain why organisms show limited plasticity (Box 1). From a pure optimality view, if the behavioral optima in two environments are very different (e.g. activity in the presence versus absence of predators), animals should have the plasticity required to exhibit the optimum in both environments. However, because organisms make unavoidable errors (e.g. due to environmental unpredictability), they might do best with a less plastic strategy. If, for example, prey have poor information about whether predators are present, they might need to play it safe and stay in or near refuge even as predators come and go [44].

Existing evolutionary models can also guide our thinking about the evolution of behavioral correlations (Box 2). One view is that these correlations reflect underlying proximate mechanisms (Box 3) that are difficult to decouple. Many of the examples presented earlier involve suboptimal behaviors (e.g. inappropriate boldness when predators are present, or excess sexual cannibalism) that seem to imply proximate constraints that maintain the correlations in spite of selection against

Box 3. Proximate mechanisms underlying behavioral syndromes

To understand behavioral syndromes, it is useful to establish the mechanistic basis for individual variation in behavioral type (e.g. determine what makes some individuals more aggressive than others in multiple contexts). In particular, we are interested in whether behavioral syndromes are governed by common or independent mechanisms. Behavioral correlations owing to a common mechanism underlying two behaviors (e.g. pleiotropic gene effects) should be more difficult to decouple than behaviors that are statistically correlated but, in fact, governed by independent mechanisms.

Recent studies of laboratory model organisms show that their behavioral type has a genetic basis. In *Drosophila*, the *for* gene underlies correlations between larval foraging activity, antiparasite behavior and adult foraging [76]. In laboratory mice [77,78] and the great tit [35–37], quantitative genetic methods documented the heritability of behavioral syndromes, and selection experiments produced correlated changes in suites of behaviors. Recent work in this area used quantitative trait locus (QTL) analysis to estimate the number and relative importance of loci affecting a syndrome. For example, Turri *et al.* [79] recently showed that ‘anxiety’ in mice might be the product of at least three behavioral tendencies (low activity, avoidance of aversive stimuli, and low exploration) governed by QTLs on separate chromosomes. The application of such analyses to behavioral syndromes in non-model organisms will represent a significant step forward in our approach to behavioral ecology.

Although numerous studies have examined the effects of individual experience on behavior, few have asked whether experience can influence a behavioral syndrome. The timing of an experience might determine its impact on a behavioral syndrome. Early behavioral ‘decisions’ as subtle as habitat choice might produce small differences in juvenile feeding and growth rates or energetic states that ultimately result in the development of a behavioral syndrome [52]. Later experiences can also mold or even dissolve a behavioral syndrome. For example, although aggressive behavior might be correlated with antipredator boldness before any experience with predators, subsequent experience with a predator can decouple this correlation. Because hormones (products of the gene x environment interaction) regularly act on multiple target tissues mediating ‘suites of correlated phenotypic traits’ [80], a neuroendocrine mechanism for behavioral syndromes seems probable. Behavioral endocrinology and ‘phenotypic engineering’ via hormonal manipulations [80] should provide useful tools to address the relationship between hormones and behavioral syndromes. For example, different coping styles (proactivity–reactivity) in house mice are associated with different neuroendocrine profiles (hypothalamic–pituitary–adrenal axis reactivity to stress) that influence not only behavior, but also disease vulnerability and stress pathology [2]. Further elucidation of the complex pathways influencing hormonal effects on behavior should reveal much about how and when behavioral syndromes are either generated or uncoupled.

them. Behavioral correlations, however, can be adaptive; that is, they can reflect alternative behavioral strategies for coping with a variable environment [2,45]. Indeed, recent work showing that populations differ in the structure of their behavioral syndromes implies that the syndromes themselves are not constrained, but can evolve (Box 2). Given that behavioral syndromes exist, how do ecological selection pressures (e.g. food level or predation risk) drive the evolution of population or species differences in average behavioral type? For example, at the population level in funnel web spiders, populations with low food availability evolved higher aggression levels across multiple contexts than did populations with a history of abundant resources [46]. In salamander larvae, populations with a history of exposure to predatory fish

evolved lower activity in the presence and absence of predators than did populations with no previous exposure to fish [47]. Interestingly, in both of these examples, population differences were reduced if there was significant gene flow among populations; that is, gene flow reduced local adaptation.

At the species level, two recent studies examined the evolution of behavioral types across multiple species in a phylogenetic context. Richardson [48] showed that, across 13 species of tadpoles, those that evolved higher activity in the absence of predators (typically associated with ephemeral, predator-free habitats) also simultaneously evolved higher activity in the presence of each of three major predators. Mettke-Hoffman *et al.* [49] quantified exploratory behavior in 61 parrot species and found (using multivariate analyses accounting for phylogeny) that the species that explore more tend to live in complex habitats (e.g. forest edges), feed on foods that take time to evaluate (e.g. nuts or fruits) or live in habitats with low predation risk (e.g. islands). The authors suggest that these associations occur because these are conditions in which more exploration either has high benefits or low costs.

A separate issue involves the maintenance of individual variation in behavioral types. This variation could be maintained by the usual evolutionary mechanisms that favor maintenance of genetic polymorphisms or additive genetic variation in plasticity (i.e. mutation–selection or migration–selection balance or overdominance) [50]. Alternatively, frequency-dependent selection could facilitate the coexistence of alternative behavioral types [51]. However, frequency dependence by itself does not predict when different individuals should show distinct behavioral types as opposed to when each individual should show a mix of strategies. In fact, in the classic hawk–dove scenario, a mix of pure hawks and pure doves is thought to be unlikely because such mixtures are usually dynamically unstable. Dall *et al.* [52] recently suggested that distinct personality types can persist and coexist when either the cost of flexibility is large, or more interestingly, when the benefit of being predictable (consistent) is large. The latter might occur if predictability enables individuals to create credible threats or promises that manipulate social partners to respond in beneficial ways. For example, if some individuals are eavesdroppers who assess the contest behaviors of each other, consistently playing hawk or dove (as opposed to being unpredictable) can reduce costly, escalated fights.

Finally, in a striking demonstration that behavioral type can influence macroevolution, Lefebvre's group found that bird taxa that had a high tendency to exhibit feeding innovations (that are associated with an exploratory, problem solving behavioral type [53]) apparently showed higher speciation rates (i.e. they were more speciose, but not more susceptible to extinction [54]). The hypothesized mechanism is that behavioral innovation (particularly in combination with social transmission of the innovation) enables populations to invade new niches, habitats or geographical ranges, ultimately resulting in speciation.

Ecological Implications

Behavioral syndromes might often have important ecological impacts because: (i) behavioral correlations and limited plasticity can generate tradeoffs that limit the ability of a species to cope with limiting environmental factors; and (ii) behavioral correlations across contexts (e.g. between reproductive, predator–prey and dispersal behaviors) can couple birth, death and dispersal processes in ways that are not usually included in ecological analyses.

For example, activity syndromes that produce a conflict between feeding and predator avoidance can limit species distributions at a landscape level [9,15,48]. In the absence of limited plasticity in activity and refuge use, a species should be able to both drastically reduce activity to cope with predators, and increase activity as much as necessary to compete well or to grow rapidly in ephemeral habitats. However, the limited plasticity associated with an activity syndrome appears to limit species to particular habitats. High activity types are typically restricted to predator-free habitats presumably because they do not reduce their activity enough to persist with predators, whereas low activity types utilize high-risk habitats probably because their maximum activity levels are not high enough to persist in ephemeral conditions or in sites with high food competition.

Limited plasticity should be a particularly important problem in rapidly changing environments, such as human-disturbed habitats. Challenged by anthropogenic environmental change, species that lack behavioral plasticity are likely to exhibit inappropriate behaviors that contribute to their decline [55]. Conversely, large-scale analyses of bird taxa suggest that more flexible, less neophobic species tend to respond more favorably to novel environments [56,57]. One strong indicator of the ability of a species to adjust to novel environments is whether it is an invasive species. A comparison of 29 pairs of closely related species of birds across four continents found that the tendency to exhibit feeding innovations (which is probably part of a general behavioral type) was strongly associated with invasiveness [56,57].

Even if most individuals exhibit limited plasticity and a poor ability to cope with environmental change, a species can still respond adequately to the change if the species harbors substantial variation in behavioral types; that is, if at least some individuals respond well. Although ecologists have shown a renewed interest in the importance of individual variation within species [8], the role of behavioral syndromes in maintaining variation in behavioral types, and the possible role of within-species variation in behavioral type in enabling species to cope with human-induced rapid environmental change, remain unstudied.

The relationship between species invasions and behavioral type also illustrates how behavioral syndromes can affect ecological interactions by coupling dispersal and other ecologically important behaviors. Invasive species are often good dispersers [58,59]. High dispersal rates have, in turn, been associated with boldness [24,25,77] that is often correlated with aggressiveness and high activity [16,19]. Thus, the dispersal process itself might

select for bold-aggressive individuals (i.e. only they disperse), which then have a particularly strong tendency to disrupt invaded communities. Dispersal is, of course, important not only in invasive species dynamics, but also in any spatially patchy scenario (e.g. metapopulations or fragmented habitats). Although there has been some recognition of the importance of behavior in spatially structured populations [60,61], further study of suites of behaviors associated with dispersal is needed.

Concluding remarks

Recent work suggests that behavioral syndromes (suites of correlated behaviors across contexts) are important because they can: (i) limit behavioral plasticity; (ii) explain non-optimal behavior; and (iii) help to maintain individual variation in behavior. In turn, these behavioral effects can have major impacts on individual fitness, species distributions, species responses to environmental change, and speciation rates. We are, however, at an early stage in quantifying and understanding the phenomenon. Most studies to date have focused on a few species, primarily in laboratory conditions. Further work with more species, particularly in the field, is needed to identify larger patterns, such as which behaviors are correlated under which conditions, and how stable syndromes and behavioral types are. These studies should also build our base of knowledge about the effects of behavioral syndromes on fitness, species performance and evolution. Simultaneously, we need explicit theory about the evolution of behavioral syndromes, and ecological theory that incorporates behavioral syndromes. Ultimately, behavioral syndromes could form a key bridge in an interdisciplinary approach that integrates proximate mechanisms (genetics, development, and neuroendocrine bases) with ecology and evolution.

Acknowledgements

This paper emerged from a graduate course and workshop at the University of California at Davis sponsored by the UCD Center for Animal Behavior and the Animal Behavior Graduate Group. Numerous participants contributed valuable ideas and insights. The work was supported by grants and fellowships from the National Science Foundation, in particular, NSF IBN-0222063 awarded to A.S., and by an Animal Behavior Society student grant.

References

- Pervin, L. and John, O.P. (1999) *Handbook of Personality: Theory and Research*, 2nd edn, Guilford
- Koolhaas, J.M. *et al.* (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* 23, 925–935
- Gosling, S. (2001) From mice to men: what can we learn about personality from animal research. *Psychol. Bull.* 127, 45–86
- Roff, D.A. (2001) *The Evolution of Life Histories: Theory and Analysis*, Chapman & Hall
- Dingle, H. (2001) The evolution of migratory syndromes in insects. In *Insect Movement: Mechanisms and Consequences* (Woiod, I.P. *et al.*, eds), pp. 159–181, CABI Publishers
- Sih, A. *et al.* Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* (in press)
- Clark, A.B. and Ehlinger, T.J. (1987) Pattern and adaptation in individual behavioral differences. In *Perspectives in Ethology* (Bateson, P.P.G. and Klopfer, P.H., eds), pp. 1–47, Plenum Press
- Bolnick, D.I. *et al.* (2003) The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* 161, 1–28
- Sih, A. *et al.* (2003) Behavioral correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Anim. Behav.* 65, 29–44
- Sih, A. (1987) Predators and prey lifestyles: an evolutionary and ecological overview. In *Predation: Direct and Indirect Impacts on Aquatic Communities* (Kerfoot, W.C. and Sih, A., eds), pp. 203–224, University Press of New England
- Werner, E.E. and Anholt, B.R. (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.* 142, 242–272
- Lima, S.L. (1998) Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive and ecological perspectives. *Adv. Study Behav.* 27, 215–290
- Maurer, E.F. and Sih, A. (1996) Ephemeral habitats and variation in behavior and life history: comparisons of sibling salamander species. *Oikos* 76, 337–349
- Sih, A. *et al.* (1988) The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. *Am. Nat.* 132, 463–483
- Brodin, T. and Johansson, F. The potential for natural selection on the growth/predation risk trade-off in a damselfly. *Ecology* (in press)
- Riechert, S.E. and Hedrick, A.V. (1993) A test of correlations among fitness-related behavioral traits in the spider, *Agelenopsis aperta* (Araneae, Agelenidae). *Anim. Behav.* 46, 669–675
- Maupin, J.L. and Riechert, S.E. (2001) Superfluous killing in spiders: a consequence of adaptation to food-limited environments? *Behav. Ecol.* 12, 569–576
- Arnqvist, G. and Henriksson, S. (1997) Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evol. Ecol.* 11, 255–273
- Huntingford, F.A. (1976) The relationship between antipredator behavior and aggression among conspecifics in the three-spined stickleback. *Anim. Behav.* 24, 245–260
- Wilson, D.S. *et al.* (1994) Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* 9, 442–446
- Coleman, K. and Wilson, D.S. (1998) Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim. Behav.* 56, 927–936
- Wilson, D.S. (1998) Adaptive individual differences within single populations. *Philos. Trans. R. Soc. Lond. Ser. B* 353, 199–205
- Godin, J.-G.J. and Dugatkin, L.A. (1996) Female mating preferences for bold males in the guppy, *Poecilia reticulata*. *Proc. Natl. Acad. Sci. U. S. A.* 93, 10262–10267
- Fraser, D.F. *et al.* (2001) Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *Am. Nat.* 158, 124–135
- Dingemanse, N.J. *et al.* (2003) Natal dispersal and personalities in great tits. *Proc. R. Soc. Lond. Ser. B* 270, 741–747
- Reale, D. *et al.* (2000) Consistency of temperament in bighorn ewes and correlates with behavior and life history. *Anim. Behav.* 60, 589–597
- Reale, D. and Festa-Bianchet, M. (2003) Predator-induced natural selection on temperament in bighorn ewes. *Anim. Behav.* 65, 463–470
- Koolhaas, J.M. *et al.* (2001) How and why coping systems vary among individuals. In *Coping With Challenges: Welfare in Animals Including Humans* (Broom, D.M., ed.), pp. 197–209, Dahlem University Press
- Benus, R.F. *et al.* (1991) Heritable variation for aggression as a reflection of individual coping strategies. *Experientia* 47, 1008–1019
- Hessing, M.J.C. *et al.* (1993) Individual behavioural characteristics in pigs. *Appl. Anim. Behav. Sci.* 37, 285–295
- Malmkvist, J. and Hansen, S.W. (2002) Generalization of fear in farm mink, *Mustela vison*, genetically selected for behaviour towards humans. *Anim. Behav.* 64, 487–501
- van Hierden, Y.M. *et al.* (2002) The development of feather pecking behaviour and targeting of pecking in chicks from a high and low feather pecking line of laying hens. *Appl. Anim. Behav. Sci.* 77, 183–196
- Verbeek, M.E.M. *et al.* (1994) Consistent individual differences in early exploratory behaviour of male great tits. *Anim. Behav.* 48, 1113–1121
- Verbeek, M.E.M. *et al.* (1996) Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* 133, 945–963
- Drent, P.J. *et al.* (2003) Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.* 64, 929–938
- van Oers, K. *et al.* (2003) Realized heritability and repeatability of

- risk-taking behaviour in relation to avian personalities. *Proc. R. Soc. Lond. Ser. B* 271, 65–73
- 37 van Oers, K. *et al.* Genetic correlations of avian personality traits: correlated response to artificial selection. *Behav. Genet.* (in press)
 - 38 Carere, C. *et al.* (2003) Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and response to social stress. *Horm. Behav.* 43, 540–548
 - 39 Carere, C. *et al.* (2001) Effect of social defeat in a territorial bird selected for different coping styles. *Physiol. Behav.* 73, 427–433
 - 40 Dingemanse, N.J.C. *et al.* (2002) Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.* 64, 929–938
 - 41 Dingemanse, N.J.C. *et al.* Fitness consequences of avian personalities in a fluctuating environment. *Proc. R. Soc. Lond. Ser. B* (in press)
 - 42 D'Eath, R.B. and Burn, C.C. (2002) Individual differences in behaviour: a test of 'coping style' does not predict resident-intruder aggressiveness in pigs. *Behaviour* 139, 1175–1194
 - 43 Soldz, S. and Valliant, G.E. (1999) The Big Five personality traits and the life course: a 45-year longitudinal study. *J. Res. Personal.* 33, 208–232
 - 44 Sih, A. (1992) Forager uncertainty and the balancing of antipredator and feeding needs. *Am. Nat.* 139, 1052–1069
 - 45 Hedrick, A.V. (2000) Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proc. R. Soc. Lond. Ser. B* 267, 671–675
 - 46 Riechert, S.E. (1993) The evolution of behavioral phenotypes: lessons learned from divergent spider populations. *Adv. Study Anim. Behav.* 22, 103–134
 - 47 Storfer, A. and Sih, A. (1998) Gene flow and ineffective antipredator behavior in a stream-dwelling salamander. *Evolution* 52, 558–565
 - 48 Richardson, J.M.L. (2001) A comparative study of activity levels in larval anurans and response to the presence of different predators. *Behav. Ecol.* 12, 51–58
 - 49 Mettke-Hoffman, C. *et al.* (2002) The significance of ecological factors for exploration and neophobia in parrots. *Ethology* 108, 249–272
 - 50 de Jong, G. and Gavrillets, S. (2000) Maintenance of genetic variation in phenotypic plasticity: the role of environmental variation. *Genet. Res.* 76, 295–304
 - 51 Maynard Smith, J. (1982) *Evolution and the Theory of Games*, Cambridge University Press
 - 52 Dall, S.R.X. *et al.* The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* (in press)
 - 53 Webster, S.J. and Lefebvre, L. (2000) Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Anim. Behav.* 62, 23–32
 - 54 Nicolakakis, N. *et al.* (2003) Behavioural flexibility predicts species richness in birds, not extinction risk. *Anim. Behav.* 65, 445–452
 - 55 Schlaepfer, M.A. *et al.* (2002) Ecological and evolutionary traps. *Trends Ecol. Evol.* 17, 474–480
 - 56 Sol, D. and Lefebvre, L. (2000) Behavioral flexibility predicts invasion success in birds introduced to New Zealand. *Oikos* 90, 599–605
 - 57 Sol, D. *et al.* (2002) Behavioral flexibility and invasion success in birds. *Anim. Behav.* 63, 495–502
 - 58 Lodge, D.M. (1993) Biological invasions: lessons for ecology. *Trends Ecol. Evol.* 8, 133–137
 - 59 Rehage, J.S. and Sih, A. Dispersal characteristics and boldness: a comparison of *Gambusia* species of varying invasiveness. *Biol. Invas.* (in press)
 - 60 Woodruffe, R. (2003) Dispersal and conservation: a behavioural perspective on metapopulation persistence. In *Animal Behaviour and Wildlife Conservation* (Festa-Bianchet, M. and Apollonio, eds), pp. 33–48, Island Press
 - 61 Stamps, J. (2001) Habitat selection by dispersers: proximate and ultimate approaches. In *Dispersal* (Clobert, J. and Danchin, E., eds), pp. 230–242, Oxford University Press
 - 62 Scheiner, S.M. (1993) Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* 24, 35–68
 - 63 DeWitt, T.J. and Scheiner, S.M. (2004) *Phenotypic Plasticity: Functional and Conceptual Approaches*, Oxford University Press
 - 64 Sih, A. (2004) A behavioral ecological view of phenotypic plasticity. In *Phenotypic Plasticity: Functional and Conceptual Approaches* (DeWitt, T.J. and Scheiner, S.M., eds), pp. 112–125, Oxford University Press
 - 65 Tufto, J. (2000) The evolution of plasticity and nonplastic spatial and temporal adaptations in the presence of imperfect environmental cues. *Am. Nat.* 156, 121–130
 - 66 Padilla, D.K. and Adolph, S.C. (1996) Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Evol. Ecol.* 10, 105–117
 - 67 DeWitt, T.J. *et al.* (1998) Costs and limits to benefits as constraints on the evolution of phenotypic plasticity. *Trends Ecol. Evol.* 13, 77–81
 - 68 Holt, R.D. (1996) Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution. *Oikos* 75, 182–192
 - 69 Lynch, M. and Walsh, B. (1998) *Genetics and Analysis of Quantitative Traits*, Sinauer Associates
 - 70 Weber, K.E. (1992) How small are the smallest selectable domains of form? *Genetics* 130, 345–353
 - 71 Cheverud, J.M. (1996) Developmental integration and the evolution of pleiotropy. *Am. Zool.* 36, 44–50
 - 72 Cheverud, J.M. (2000) The genetic architecture of pleiotropic relations and differential epistasis. In *The Character Concept in Evolutionary Biology* (Wagner, G., ed.), pp. 411–433, Academic Press
 - 73 Wagner, G.P. *et al.* (2000) Developmental evolution as a mechanistic science: the inference from developmental mechanisms to evolutionary processes. *Am. Zool.* 40, 819–831
 - 74 Hedrick, A.V. and Riechert, S.F. (1989) Genetically-based variation between two spider populations in foraging behavior. *Oecologia* 80, 533–539
 - 75 Palmer, J.O. and Dingle, H. (1989) Responses to selection on flight behavior in a migratory population of milkweed bug *Oncopeltus fasciatus*. *Evolution* 43, 1805–1808
 - 76 Sokolowski, M.B. (2001) *Drosophila*: genetics meets behavior. *Nat. Rev. Genet.* 2, 879–892
 - 77 Sluyter, F. *et al.* (1995) A comparison between house mouse lines selected for attack latency or nest-building: evidence for a genetic basis of alternative behavioral strategies. *Behav. Genet.* 25, 247–252
 - 78 Bult, A. and Lynch, C.B. (2000) Breaking through artificial selection limits of an adaptive behavior in mice and the consequences for correlated responses. *Behav. Genet.* 30, 193–206
 - 79 Turri, M.G. *et al.* (2001) QTL analysis identifies multiple behavioral dimensions in ethological tests of anxiety in laboratory mice. *Curr. Biol.* 11, 725–734
 - 80 Ketterson, E.D. and Nolan, V. Jr (1999) Adaptation, exaptation, and constraint: a hormonal perspective. *Am. Nat.* 154, S4–25