

## REVIEW AND SYNTHESSES

### Ecological implications of behavioural syndromes

Andrew Sih,<sup>1\*</sup> Julien Cote,<sup>2†</sup> Mara Evans,<sup>3</sup> Sean Fogarty<sup>4</sup> and Jonathan Pruitt<sup>5‡</sup>

#### Abstract

Interspecific trait variation has long served as a conceptual foundation for our understanding of ecological patterns and dynamics. In particular, ecologists recognise the important role that animal behaviour plays in shaping ecological processes. An emerging area of interest in animal behaviour, the study of behavioural syndromes (animal personalities) considers how limited behavioural plasticity, as well as behavioural correlations affects an individual's fitness in diverse ecological contexts. In this article we explore how insights from the concept and study of behavioural syndromes provide fresh understanding of major issues in population ecology. We identify several general mechanisms for how population ecology phenomena can be influenced by a species or population's average behavioural type, by within-species variation in behavioural type, or by behavioural correlations across time or across ecological contexts. We note, in particular, the importance of behavioural type-dependent dispersal in spatial ecology. We then review recent literature and provide new syntheses for how these general mechanisms produce novel insights on five major issues in population ecology: (1) limits to species' distribution and abundance; (2) species interactions; (3) population dynamics; (4) relative responses to human-induced rapid environmental change; and (5) ecological invasions.

#### Keywords

Animal personalities, behavioural syndromes, dispersal, distribution and abundance, ecological invasions, environmental change, intraspecific variation, population dynamics, spatial ecology, species interactions.

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#### INTRODUCTION & GOALS

Ecology has a long history of incorporating animal behaviour into analyses of ecological patterns and dynamics (Sutherland 1996; Fryxell & Lundberg 1998). Over the years, numerous articles have used optimality theory to explain forager diets, habitat use and predator avoidance that underlie predator-prey and competitive interactions that, in turn, potentially explain major patterns in population and community ecology (Valdovinos *et al.* 2010). A theme of this work is that classic issues like predator impacts on prey, competitive coexistence, or trophic cascades can often only be understood fully if we account for the behaviours of key species (Schmitz *et al.* 2008). Recent articles further emphasise behaviour's role in applied ecological issues like ecological invasions or relative species abilities to cope with human-induced rapid environmental change (Sih *et al.* 2011).

Herein, we focus on ecological insights that come from the new emphasis in animal behaviour on behavioural syndromes (a.k.a. animal personalities) that acknowledges that in many species, individuals

exhibit both within-individual and between-individual consistency in behaviours across time or across ecological contexts (Sih *et al.* 2004; Dall *et al.* 2004; Sih & Bell 2008). In many species, some individuals are consistently the more aggressive behavioural type (BT), whereas others are consistently less aggressive not just in competitive contests that involve aggression, but also in foraging, mating, parental and/or antipredator behaviour (Riechert & Hedrick 1993). Other documented BT axes include variation in boldness (Wilson *et al.* 1994) or sociability (Cote *et al.* 2010a). Although it has long been clear that humans differ in personality, and that a few other animals (e.g. primates, dogs, cats, laboratory rodents) exhibit consistent individual BTs, recent work suggests that behavioural syndromes apply across the entire animal kingdom (Gosling 2001).

Behavioural syndromes are ecologically important because an individual's BT can clearly affect its fitness (Smith & Blumstein 2008; Biro & Stamps 2008). When different BTs are favoured in different environments, the existence of BTs can result in suboptimal behaviour in some environments. For example, individuals with a bold BT often take unnecessary risks and suffer high mortality in dangerous

<sup>1</sup>Department of Environmental Science and Policy, University of California at Davis, 95616, USA

<sup>2</sup>Department of Environmental Science and Policy, University of California at Davis, 95616, USA

<sup>3</sup>Department of Evolution & Ecology, University of California at Davis, 95616, USA

<sup>4</sup>Department of Environmental Science and Policy, University of California at Davis, 95616, USA

<sup>5</sup>Department of Environmental Science and Policy, University of California at Davis, 95616, USA

\*Correspondence: E-mail: asih@ucdavis.edu

<sup>†</sup>Current address: CNRS, EDB (Laboratoire Evolution et Diversité Biologique), UMR 5174, Toulouse, France, and Université de Toulouse UPS, Laboratoire Evolution et Diversité Biologique, 118 Route de Narbonne, Bât. 4R3, 31062 Toulouse Cedex 9, France, julien.cote@cict.fr

<sup>‡</sup>Current address: Department of Biological Sciences, 213 Clapp Hall, University of Pittsburgh, Pittsburgh, PA 15260, USA, agelenopsis@gmail.com

environments, whereas more cautious individuals are often unnecessarily cautious and miss out on opportunities in safer situations (e.g. Sih *et al.* 2003). Hallmarks of the behavioural syndrome concept include limited plasticity (relative to infinite, optimal plasticity) and behavioural correlations (carryovers across ecological contexts or across time). Both these phenomena can generate conflicts or trade-offs (Sih *et al.* 2004). Although ecologists are familiar with the notion that a species' fixed traits (e.g. a fixed morphology) can generate ecologically important trade-offs, recent work on behavioural syndromes emphasises that animals also often have less than optimal behavioural plasticity that has analogous effects.

Although numerous recent studies have quantified behavioural syndromes, their genetic and neuroendocrine bases (Koolhaas *et al.* 2007; van Oers & Mueller 2010), and their effects on fitness, an exciting new frontier that is only now getting attention examines implications of behavioural syndromes for major issues in ecology (Reale *et al.* 2007). Herein, we provide an organising framework for this growing field. We focus on population ecology (including interactions involving 2–3 species). A future article will address community/ecosystem issues.

Species' distribution and abundance and population dynamics are often heavily influenced by species interactions – competition, predation, parasitism and/or mutualism – that are often mediated by spatial and/or temporal environmental variation. Understanding limits to distribution and abundance and species interactions are more important than ever in a world where human-induced rapid environmental change (HIREC) is putting most organisms into novel situations with new limiting factors and in some cases, releases from previous limiting factors. Some species are responding poorly to HIREC, whereas others are expanding their ranges (e.g. invasive species).

In Box 1, we outline three main ways that behavioural syndromes affect ecological issues. Below, we discuss how these mechanisms yield important insights for understanding: (1) species performance and limits to distribution and abundance; (2) species interactions; (3) population dynamics; (4) responses to environmental change and (5) ecological invasions.

## SPECIES PERFORMANCE AND LIMITS TO DISTRIBUTION AND ABUNDANCE

### Behavioural correlations and effects of a species' average BT

A classic idea in ecology is that species distributions and abundances are ultimately limited by trade-offs, often associated with relatively fixed traits; e.g. being heavily armoured can enhance survival where predators are present, but at a cost of reduced foraging efficiency and competitive ability. Although behaviours are inherently plastic, behavioural trade-offs often occur due to what Sih *et al.* (2004) called *within-situation* time budget conflicts; e.g. more time spent active helps garner resources, but often exposes the active forager to more risk. Time budget conflicts can limit species abilities to cope simultaneously with both predation and competition, and can thus limit species distributions or abundances. Importantly, this trade-off exists even if individuals exhibit optimal plasticity with no behavioural syndrome.

Behavioural syndromes offer a novel twist on this core idea by providing an *across-situation* trade-off. Individuals (populations, or species) that are more active (bold or aggressive) than others and thus thrive in the absence of predators also carryover to be more

active (bold or aggressive) than others *at a later time or place* in the presence of predators (Sih *et al.* 2003). The limited plasticity associated with having a BT can thus generate a conflict that can limit population success. For example a standard dogma is that in permanent waters with predatory fish, prey (e.g. tadpoles or macroinvertebrates) exhibit low activity and high refuge use whereas in ephemeral habitats without predatory fish, related prey exhibit a more active, faster lifestyle (Sih 1987). High activity prey are too bold to persist with fish, and low activity prey are outcompeted or unable to complete their larval period quickly enough to persist in ephemeral habitats. The fact that prey transplanted from low to high predation pressures or *vice versa* often do not exhibit appropriate plasticity, but instead carry over a BT that makes them unable to persist in the other predation regime reflects the behavioural correlations across predation regimes, and limited plasticity inherent in the behavioural syndrome concept.

Beyond trade-offs associated with positive correlations between activity, boldness and aggressiveness, recent studies on animal personalities also point out potentially important behavioural correlations that ecologists have less often considered. One example involves an association between aggressiveness, boldness and a general proactive coping style characterised by low environmental sensitivity and a poor ability to respond behaviourally to environmental change (Koolhaas *et al.* 2007). Another example that will be discussed in detail later in the article is the existence of correlations between BT and dispersal tendency.

Behavioural correlations that produce trade-offs that can limit species success are particularly powerful if they represent constraints that cannot be modified by natural selection. Recent studies, however, have detected variation in key behavioural correlations. For example, although boldness with predators present is positively correlated with aggressiveness towards conspecifics in populations of sticklebacks that have experienced heavy predation pressure, this correlation is not seen (or might even be weakly negative) in populations under lower predation pressure (Bell & Sih 2007; Dingemanse *et al.* 2007, 2010). Thus, in high predation sites, selection favouring low boldness also results in low aggressiveness that typically reduces competitive ability. In contrast, in low predation sites, selection favouring higher boldness does not necessarily affect aggressiveness. Along similar lines, although ecologically important aggressiveness is often correlated across multiple contexts (e.g. Duckworth 2006; Pruitt *et al.* 2008), this is not always true (Holway *et al.* 1998) and even more strikingly, the direction of the correlation can differ among systems. More aggressive individuals sometimes spend so much time in aggressive interactions that they forage less than less aggressive individuals, but in other cases, aggressiveness and foraging activity are positively correlated (Pintor *et al.* 2009). Quantifying the direction and magnitude of correlations among ecologically relevant behaviours is thus crucial for understanding trade-offs that can explain species success.

### Variation within species in BT

Within species variation in BT should, in principle, allow species to cope with a broader range of environmental conditions via mechanisms that are analogous to the role of genetic variation in allowing evolutionary responses to different environments. However, unlike genetic variation *per se* which can be selectively neutral, variation in BT (genetic or not) is a key functional aspect of the species' ecology. Having within-species genetic variation in BT can reduce short-term

### Box 1 An introduction to three main ways that behavioural syndromes affect ecological issues

Although most of the recent literature on behavioural syndromes looks at variation in BT among individuals within a population, one can also apply the concept to consistent differences in BT among populations within a species, or among species. We thus discuss ecological insights associated with effects of: (1) a species' average BT, (2) variation in BT within the species (both variation among individuals within populations and variation among populations); and (3) behavioural syndromes (behavioural correlations) both within and across species.

The idea that species differ in average BT and that these differences are ecologically important is familiar to ecologists. Some species are more aggressive, bolder, or more social, than others (e.g. Blumstein 2006). A species' basic BT is an important species trait that can have major effects on its ecological role and impact on a community (e.g. Holway & Suarez 1999). Herein, we briefly review these familiar ideas with a particular focus on novel insights associated with acknowledging that species differ in average BT.

The idea that variation in BT within a species matters is related to a familiar idea in evolution and ecology – that genetic variation matters, in particular in allowing a species to respond evolutionarily to changing environments. Here, we focus on variation in a key, heritable, ecologically important trait – the individual's BT. One simple point is that having more variation in BT allows a species to do well in a broader range of conditions. A parallel point is that greater diversity in BTs within a species can allow a single species to function like multiple species in its effects on the community or ecosystem. Bolnick *et al.* (2011) summarised general reasons why intraspecific trait variation can matter in community ecology; herein, we focus on intraspecific variation in BT and specific ways that it can be important for population ecology.

Finally, we discuss how behavioural correlations across time and space, or across ecological conditions, can have ecologically important effects. Our view is that behavioural syndromes (e.g. correlations between foraging, antipredator, reproductive and/or dispersal behaviours) produce correlations among demographic rates (births, deaths, and movements among patches) that carryover across time or across situations. Some of these correlations are part of standard ecological dogma – e.g. the fact that bolder BTs tend to have higher resource intake rates (and thus higher birth rates) and take greater risks (and thus suffer higher death rates). Here, we highlight other lesser known, demographic correlations that arise from behavioural syndromes. More details on mechanisms are summarised in Table 1 and discussed with examples in the main text.

success in a particular current environment (since some genotypes are not as well adapted), but should increase long-term success and in particular, reduce the likelihood of local extinction. This can allow the species to do well in broader range of habitats (spatial variation) and across a broader range of temporal variation. In essence, having variation among individuals in BT within a species reduces the importance of the trade-off that limits performance for a given BT.

For example, a species that has both bold individuals (or populations) that thrive in environments without risk, and cautious individuals (or populations) that cope well with high risk can potentially do well in both ecological conditions (Sih *et al.* 2003). The species' overall success is then limited by mechanisms that reduce variation within populations (e.g. strong selection) or among populations (e.g. gene flow). Another example involves density-dependent variation in fitness. In some systems, more aggressive individuals outcompete others at high density, but at low density, aggressiveness is a wasted, costly effort (Duckworth 2006). In other cases, asocial individuals do well at low density, whereas more social individuals thrive at high density (Cote & Clobert 2007; Pruitt & Riechert 2009). In r-K terms, often, the BTs that do well at low density have high r, but low K, while BTs that do well at high density have low r and high K. Having both BTs with density-dependent frequencies can increase both r and K for the overall species.

Wider variation in BT can be particularly important if individuals with different BTs have complementary roles with positive synergistic effects; e.g. cooperation among individuals with different roles that are critical for group success (e.g. in humans, eusocial insects or social spiders (Beshers & Fewell 2001)). The frequency of the different BTs and how the mix interacts can be critical for group (colony) success. For instance, in the social spider *Anelosimus studiosus*, colony members exhibit either an aggressive/asocial or docile/social BT. Aggressive

individuals benefit colonies by facilitating the capture of large prey and deflecting colony-level predators and parasites (Pruitt & Riechert 2011a). Docile females benefit colonies by reducing within-colony agonism (Pruitt & Riechert 2009) and by consuming uneaten prey (Pruitt & Riechert 2011b) that otherwise attract ants, which harm colonies and limit colony distributions (Purcell & Aviles 2008). As in social insect societies (Muller & Chittka 2008), colonies with mixed BTs experience the greatest fitness (Pruitt & Riechert 2011b).

Finally, wider variation in BTs can increase the prevalence of *keystone individuals* that have particularly large (positive or negative) effects on overall population performance (Sih & Watters 2005). Positive impacts of keystone individuals involve enhanced spread of information or innovations that are critical for a species to adjust to a changing environment (e.g. in humans Burt 2004). Recent studies emphasise the importance for facilitating information flow of the personality of key individuals in the social network (Krause *et al.* 2010). Alternatively, keystone individuals can enhance group cohesion and stability that can be important for group success. Keystone individuals can also have strong *negative* impacts on the overall group; e.g. 'superspreaders' of disease, or hyper-aggressive individuals that drive others into hiding and thus reduce mating activity (Sih & Watters 2005).

## SPECIES INTERACTIONS

### Effects of average species BT and within-species variation in BT

BTs can clearly affect the *strength* of species interactions. Bold/aggressive predators have greater impacts (than less bold/aggressive predators) on prey (Pruitt & Krauel 2010); conversely, bold prey suffer heavier predation (Sih *et al.* 2003). Depending on the parasite, hosts with bold, aggressive, exploratory, or sociable BTs can be more

heavily parasitised (Barber & Dingemanse 2010; Kortet *et al.* 2010). When parasites manipulate host BTs, a positive feedback loop can emerge where: (1) host BT affects the likelihood of initially picking up parasites; (2) parasites then manipulate host BTs (often making them even more active, bold, aggressive or sociable) to increase their probability of being consumed by the next host in a complex life cycle; and (3) the manipulated host BT is also more likely to acquire even more parasites. Parasite manipulation of host BTs thus often has the indirect effect (where one species alters the strength of interaction between two other species) of substantially increasing predation on hosts (Lafferty & Morris 1996). Another example of an indirect effect mediated by BT involves the owl limpet, *Lottia gigantea* where aggressive BTs so fiercely guard territories that these sites are herbivore-depauperate refugia for palatable algae (Shanks 2002).

BTs can also influence *which species interact*. In spiders, bold/aggressive individuals have broader diets; i.e. impact a broader range of prey (Riechert 1991). Boldness also influences the kinds of parasites acquired by individuals (Wilson *et al.* 1993). In domestic cats, feline immunodeficiency virus (FIV) is transmitted through agonistic interactions, whereas feline leukaemia virus (FeLV) is transmitted via affiliative interactions. Accordingly, more aggressive cats tend to have higher FIV, but lower FLV prevalence (Pontier *et al.* 1998).

The fundamental nature of a species interaction (e.g. whether two species are competitors or mutualists) can shift depending on a species' BT. This adds to recent literature emphasising context-dependent species interactions (Stachowicz 2001). For instance, among reef fishes, although cleaner fish are usually mutualists with other species, for aggressive dusky damselfish, *Stegastes adustus*, having cleaner fish nearby actually diminishes territory owners' foraging success, owing to increased time spent fending off heterospecific 'invaders' who come to be cleaned (Arnal & Cote 1998). Similarly, ant-acacia interactions depend on ant BTs: although highly aggressive ants are effective at defending plants from herbivory, some aggressive ants also destroy flowers and effectively castrate their host plants (Yu & Pierce 1998).

Given that species interactions depend on BTs, within-species variation in BT can make one species function like multiple species with different BTs engaging in different species interactions (Bolnick *et al.* 2011); e.g. in an omnivore, more bold/aggressive BTs might be carnivorous predators that forage actively away from refuge, whereas shy/unaggressive individuals might be herbivores that stay in a vegetation refuge.

BTs can also potentially influence predator-prey interactions by altering the relative strength of consumptive (CE) vs. non-consumptive effects (NCE) of predators on prey. Recent work suggests that NCEs (e.g. costs of avoiding predators) can be as or more important than CEs (Preisser *et al.* 2005). Prey BTs can shape the magnitude of CEs vs. NCEs: fearful prey exhibit greater predator avoidance and larger NCEs, whereas bolder prey show less avoidance and greater CEs. The relative importance of CEs vs. NCEs can also depend on the predator's BT. Perhaps counter-intuitively, active predators that produce diffuse, low-intensity cues, elicit small NCEs and larger CEs, whereas less active, sit-and-wait predators that produce infrequent high-intensity cues, elicit heightened prey avoidance, and thus greater NCEs and weaker CEs (Preisser *et al.* 2007).

Finally, effects of BTs on species interactions can affect ecosystem services. For example, for seed dispersal, in hornbills, individuals differ in their tendency to travel across patchy landscapes: some primarily disperse seeds locally, whereas others disperse seeds over longer distances (Lenz *et al.* 2011). As the matrix between habitat

patches becomes more urbanised, we might expect primarily bold/active/aggressive BTs to move across these landscapes. Shy BTs might require corridors and reduced acoustic pollution to allow dispersal. For pollination, in honey bees, tendency to forage, transport and hoard pollen are correlated, heritable, BT-related traits that influence workers' foraging decisions and colonies' efficiency as pollinators for crops (Cane & Schiffhauer 2001). In bumble bees, individual variation in a speed-accuracy continuum from 'fast-and-sloppy' to more 'slow-and-precise' foraging (Chittka *et al.* 2009) has implications for flower visitation. The presence of fast-and-sloppy individuals may facilitate the persistence of low-nectar (i.e. unrewarding/cheating) flowers (Wright & Schiestl 2009).

## Behavioural correlations

Behavioural correlations underlie classic trade-offs (e.g. between competitive ability vs. ability to cope with predators (Sih *et al.* 2003), or between competitive dominance vs. speed of discovery of ephemeral resources that influence relative species success in different species interactions). A breakdown of behavioural correlations can thus result in one species dominating in a diversity of environments. For example, in fire ants (*Solenopsis invicta*), a decoupling of intra- and interspecific aggressiveness allows workers from polygyne (i.e. multi-queen) colonies to recognise and tolerate foreign polygyne queens and neighbouring polygyne colonies (Keller & Ross 1998), while maintaining extremely high aggressiveness towards monogyne colonies and heterospecifics. Thus, in a variety of habitats throughout *S. invicta*'s introduced range, polygyne colonies attain high densities, altering ant communities and diminishing ant diversity (Gotelli & Arnett 2000).

In spatial ecology, a key correlation is between BT and dispersal behaviour, where BT-dependent dispersal (e.g. a tendency for bolder individuals to disperse more readily) creates systematic, ecological 'founder effects' that can influence species interactions in post-dispersal habitats. At a small scale, in species that exhibit ontogenetic habitat shifts, BT-dependent dispersal can influence post-shift species interactions; e.g. in bluegills, bold/aggressive fish may be the first to shift out of protective vegetation and into open water where their bold/aggressive BT may result in particularly large impacts on open water prey. Similar effects can occur whenever species recolonise ephemeral or disturbed habitats. For example, the efficacy of biocontrol agents that recolonise crop fields can be enhanced when aggressive individuals (that have larger impacts on prey) disperse more than others from natal habitats into adjacent crop fields (Bishop & Riechert 1990).

Behavioural type-dependent dispersal can be influenced by species interactions in the source habitat. When predation risk induces prey dispersal, more cautious, less aggressive prey might leave to get away from predators. Assuming a BT carryover where these prey remain cautious even in predator-free sites, this should reduce impacts prey have in the new sites. In contrast, if cautious prey hide in refuge instead of dispersing from predator sites, while bolder prey actively disperse away from predators, then these prey should have greater community impacts in the colonised site than one would otherwise expect.

## POPULATION DYNAMICS

Ecological theory (Scheiner & Willig 2010) suggests that key factors that influence population dynamics include: (1) density-dependence

which tends to enhance stability and reduce fluctuations; (2) time lags which tend to destabilise populations; (3) age/stage structure, or more generally, the existence of categories of individuals that differ in demographic parameters; and (4) spatio-temporal asynchrony which allows broad scale population stability despite local instability. Herein we discuss effects of behavioural syndromes on each of these population dynamic mechanisms.

### Effects of average BT

A classic idea is that a population's average aggressiveness has important effects on density-dependence and population regulation. Scramble competition with no aggression (where resources are thus relatively evenly distributed among individuals) can be destabilising, particularly if time lags allow populations to go well above carrying capacity. Scramble competitors can then drastically over-consume resources leading to a population crash. In contrast, more aggressive species that engage in interference competition should produce stronger density-dependence and tighter population regulation.

In many species, size-dependent aggression and interference can escalate to cannibalism (Polis 1981) which has important density-dependent impacts on population dynamics (Claessen *et al.* 2004). Cannibalism rates depend on BTs: bold/aggressive individuals often cannibalise more than shy/less aggressive ones (e.g. Pruitt *et al.* 2008). Andersson *et al.* (2007) outline an intriguing feedback where cannibalism stabilises population dynamics, this stabilisation favours resource polymorphisms within a species including a cannibal class (likely, bolder and more aggressive) and a 'prey' class (cautious and less aggressive), and the existence of multiple morphs/BTs further reinforces cannibalism possibly further stabilising population dynamics (Claessen *et al.* 2004).

Another major mechanism of density-dependent population regulation involves aggregation which can depend on the species' average sociability. Aggregation produces higher mean densities and thus potentially stronger competition, density dependence and population regulation. Aggregation can have especially important stabilising effects in host-parasite and predator-prey systems (Murdoch & Stewart-Oaten 1989). Predator aggregation in some patches (whether those are areas of high prey density or not) results in a partial refuge for prey in other patches. If both predators and prey are each highly social, as in Serengeti lions and their prey, we may see reduced predation rates and enhanced predator-prey stability relative to random mixing (Fryxell *et al.* 2007). Although aggregations might often consist of more sociable individuals that tend to be less aggressive, aggregations around resources can still lead to high levels of aggression in less social species.

Finally, recent work by Reale *et al.* (2010) connects BTs, life histories and physiology together in 'pace of life' (POL) syndromes that parallel r-K life history syndromes. Fast POL species tend to exhibit high aggression, boldness, activity and dispersal rates, with low parental care and sociability and superficial exploration. A fast POL is also associated with a physiology that maintains high activity without investing in antipredator behaviour or disease resistance. Fast POL individuals are geared towards quickly finding and extracting resources, and converting those resources into offspring, without regard for risks such as predation or illness. This bold/aggressive BT is tied to a brief life with a high growth rate and early reproduction, all of which contribute to rapid generation times, high potential population growth rates, and a tendency to undergo unstable,

population fluctuations. Conversely, slow POL species are associated with K-type life histories and more stable population dynamics. Note that the POL hypothesis associates aggressiveness with a fast, r-type life history and higher population fluctuations, while the earlier discussion of density-dependence associates aggressiveness with stronger density-dependence and better regulated populations. Further empirical work is clearly needed to test these contrasting predictions.

### Behavioural correlations

Behavioural correlations *across time* can generate time lags that can induce cyclic or chaotic dynamics in simple population models; i.e. instead of responding instantaneously to changes in density (or other key factors), individuals with a BT exhibit behavioural consistency that carries over across time. BTs are known to differ in speed of response to environmental change. Along an axis of coping styles (Koolhaas *et al.* 2007), reactive individuals are, by definition, faster to sense changes and shift behaviour. In contrast, proactive individuals exhibit set, behavioural routines that should result in longer behavioural time lags (before responding to environmental changes) that are associated with greater density fluctuations.

Behavioural correlations *across context* can also influence population dynamics via effects on density-dependence, particularly when behaviours that determine local density (and thus interaction rates) are correlated to behaviours that influence the intensity of density-dependent interactions. For example, a positive correlation between aggression and activity (e.g. Pintor *et al.* 2009) can increase the strength of density-dependence because high activity increases interaction rates between aggressive individuals. More complex dynamics can arise when behavioural correlations influence density-dependence in two-species population dynamics. For example, predator-prey dynamics can depend on coupled changes in prey density and in the relative frequency of 'bold' prey (Yoshida *et al.* 2007). Relatively high densities of prey correlate with high frequencies of bold, easy to catch prey, and *vice versa* (see the next section for further discussion). Given that boldness is often positively correlated to aggressiveness, this suggests that predator-prey cycling may lead to high density patches with a high frequency of not just bold, but also aggressive BTs. The population dynamic consequences of such a situation have not yet been explored.

Finally, adaptive correlations between BT-dependent performance and dispersal can have important effects on population dynamics (Cote & Clobert 2007). For example, if patches that would be sinks for the average BT are preferentially colonised by BTs that perform well in those patches, this should allow greater landscape level population survival. In general, BT-dependent dispersal may be a key in allowing both higher colonisation success and lower extinction rate in metapopulations than would be expected from BT-independent dispersal.

### Within-species variation in BT

When BTs differ in their pattern of density-dependent fitness or dispersal, then within-population variation in BTs combined with time lags can lead to coupled oscillations in population density and in the frequencies of different BTs (Sinervo & Calsbeek 2006). Changes in density drive changes in the relative frequencies of BTs that feed back

to further change population densities in ways that again change the frequencies of BTs etc. A classic example of this dynamic is the Chitty (1960) hypothesis that suggests that long-term, cycles in the abundance of microtine rodents can be explained by a coupling of individual variation in social BT (aggressiveness, sociability and BT-dependent dispersal) and time lagged, density-dependent dispersal and reproductive output. In a more recent twist, Sinervo *et al.* (2000) found that lizards display coupled eco-evolutionary dynamics with cycling involving three different BT-related morphs replacing each other in what the authors have termed a rock-paper-scissors dynamic.

For predator-prey interactions, several mechanisms influencing dynamics involve frequency or density-dependent predation on multiple prey types; i.e. heavier predation on more common prey types, and reduced predation on rare types. This tends to enhance predator-prey coexistence and stability; or with time lags, generate predator-prey cycles. Although to date, these mechanisms have focused on multiple prey *species* or *morphs*, the basic logic should also apply to within-species variation in prey BTs.

One mechanism involves 'predator switching' where individual predators switch to preferentially feed on whichever prey type is more common (Murdoch 1969). Predator switching among prey with different BTs in one prey species should occur if different predator tactics are required to feed efficiently on different BTs. For example, if bold vs. cautious prey (or social vs. asocial prey, or more vs. less exploratory prey) forage in different habitats, or use different escape tactics, then efficient predators should specialise on whichever habitat has more prey, or whichever attack mode better fits prey that are more abundant (Murdoch 1969). If predators consistently switch to predate more heavily on more common prey BTs and ignore rare prey BTs, this should tend to stabilise predator-prey interactions (Murdoch 1969) and facilitate coexistence of multiple prey BTs. If there are time lags in predator switching (e.g. if predators need time to learn to forage effectively on the more common prey BT), this should lead to cyclic dynamics in the frequency of prey BTs.

A second mechanism involves a feedback loop where the density and relative frequencies of different prey BTs affect predator population growth rates, and in turn, predator abundance affects the relative fitness of different prey BTs. A key is a trade-off among prey types between competitive ability and predator avoidance ability. Theoretical and experimental work on rotifer-algae and bacteria-phage systems show that with this trade-off, the frequency distribution of defended vs. undefended prey types evolves rapidly with changing predator density (Meyer *et al.* 2006). Intriguingly, total prey density can remain relatively constant while the frequencies of defended and undefended prey types cycle asynchronously. Furthermore, predator densities still oscillate; increasing when undefended prey types are common, and decreasing when defended prey become more common (Yoshida *et al.* 2007). These 'cryptic cycles,' where predator density oscillates while total prey density remains constant, contrast with monotypic prey populations, where both predator and prey densities show high amplitude, out of phase, oscillations. To date, this field has not invoked prey BTs; however, BTs clearly exhibit this trade-off (e.g. bolder, more active, more exploratory prey gather more resources, but suffer higher risk), thus variation in BTs should also, in principle, generate these dynamics.

Finally, if we account for variation in BT in *both predators and prey*, this can produce oscillating population dynamics driven by coupled changes in the relative frequency of BTs in *both* species. The

underlying mechanism might involve, for example, the situation where prey with more active BTs are more likely to fall victim to less active, sit-and-wait predatory BTs, whereas inactive prey are more likely to be detected and subdued by active predator BTs (Scharf *et al.* 2006). We recently examined this BT  $\times$  BT interaction using predatory sea stars (*Pisaster ochraceus*) and prey snails (*Chlorostoma funebris*) (Pruitt *et al.*, provisionally accepted). Active *P. ochraceus* tend to capture inactive, non-fearful prey, whereas inactive *P. ochraceus* tend to capture active, fearful prey. The performance of predator BTs thus depends on the BT composition of their prey and *vice versa*. (1) When predators are mostly the active BT, they preferentially kill inactive prey, which favours more fearful, active prey; (2) the frequency of active prey BTs then increases. (3) This favours inactive predator BTs that can ambush active prey without the costs of searching; however, (4) when inactive predators become more common, this favours inactive prey, which in turn favours active predators. Such BT  $\times$  BT effects can be important in maintaining trait diversity within multiple interacting populations via multi-species, fluctuating frequency-dependent selection (Sinervo & Calsbeek 2006).

The effects of this predator-prey BT  $\times$  BT interaction on population dynamics has not yet been studied; however, analogous work on the eco-evolutionary dynamics of a system with two predator types and two prey types that trade-off prey competitive ability with predation by one or both predator types found that the resulting population dynamics can be quite complex (Ellner & Becks 2011). When the different prey types are each defended against a specific predator type, populations oscillate in ways very different from simple food chains or more general two-predator food webs. Overall, work on multiple prey species (or morphs) suggests that further studies on effects of within-species variation in prey (and predator) BTs on predator-prey dynamics should prove rewarding.

## RESPONSE TO NOVEL ENVIRONMENTS AND ENVIRONMENTAL CHANGE

A critical ecological and evolutionary issue is the need to better understand organismal responses to human-induced rapid environmental change (HIREC) that often puts organisms in evolutionarily novel conditions (Sih *et al.* 2011). HIREC includes habitat change (loss, fragmentation), exposure to novel species associated with ecological invasions, increased human harvesting and exposure to novel abiotic conditions (e.g. chemical, light, or noise pollution; climate change). Species differ strikingly in their ability to cope with HIREC. Even within the same genus, some species are doing poorly (and are thus species of conservation concern), whereas others are invasive or urbanised pests (e.g. Rehage *et al.* 2005). Behaviour is a key first response to HIREC that can potentially explain variation in performance relative to HIREC. Behavioural responses to HIREC include: (1) coping with novel 'enemies' (e.g. novel predators, competitors, diseases) and novel abiotic stressors; (2) adopting novel resources (e.g. new habitats, new foods such as crops); and (3) adjusting timing of events (e.g. timing of migration or reproduction) or space use (e.g. movement patterns) to better fit new spatiotemporal conditions (Tuomainen & Candolin 2010). A better understanding of this variation in behavioural response to HIREC can help either aid declining species or better manage invasive or pest species. Here, we discuss how accounting for behavioural syndromes can yield insights on response to environmental change.

## Effects of average BT

A standard idea is that greater behavioural flexibility should enhance response to novel situations. Recent articles indeed show that species with an average BT that is more exploratory, flexible, better at learning and/or more innovative tend to be more invasive at a large geographic scale, and/or more likely to become urbanised (Sol *et al.* 2002). One likely mechanism is that less neophobic, more exploratory individuals forage more effectively on novel prey (e.g. Sol *et al.* 2002; Rehage & Sih 2004) and/or are better at finding shelter in novel habitats. Conversely, species with relatively inflexible, neophobic BTs tend to avoid novel environments.

Other BT axes that are not inherently associated with flexibility can also affect responses to HIREC in a context-dependent way; e.g. more cautious prey tend to respond to a broad range of predators including novel predators. Or, more aggressive, voracious consumers are more likely to be catholic in their tastes and willing to attack a broad range of novel prey.

Boldness per se also influences behavioural responses to novel (e.g. urban) habitats. Using flight initiation distance (the distance that animals allow humans to approach before fleeing) as a measure of boldness, recent studies found that urban birds tend to be bolder than rural counterparts (Evans *et al.* 2010; Moller 2010) and that cautious species (that flee before humans come close) are more susceptible to human disturbance and more likely to exhibit declining population sizes (Moller 2008). Boldness can be beneficial in urban landscapes because it is related to higher foraging success (Short & Petren 2008). Boldness, however, can be detrimental if novel environments are actually dangerous. Inappropriate boldness is often a key problem for reintroductions of animals reared in captivity; e.g. Bremner-Harrison *et al.* (2004) found that bolder foxes died earlier after re-introduction. Similarly, numerous (but not all) studies have found that hatchery-reared fish tend to be bolder and/or more aggressive than wild fish, and that their weak antipredator behaviour contributes to poor survival after release (Conrad *et al.* 2011).

The fact that BT can influence reintroduction success suggests the value of screening to identify individuals that have BTs that are well suited for reintroduction (Bremner-Harrison *et al.* 2004). If BTs are shaped by experience, reintroduction programmes can train individuals to produce BTs that are more ready to cope with challenges faced after release (Conrad *et al.* 2011).

Introductions of biocontrol agents into novel habitats involve related, but more complex BT issues. Successful biocontrol agents have a large negative impact on target pests while having minimal negative impact on non-target organisms. To have large negative effects on pests, biocontrol agents should have high per capita attack rates on prey (via high activity, boldness or aggressiveness; e.g. Pruitt *et al.* 2008), but also the tendency to aggregate (associated with low aggressiveness and high sociability) particularly in areas with more pests (Murdoch & Briggs 1996). Biocontrol agents need to be flexible enough to cope with novel habitats, but to minimise non-target effects, not so flexible that they will switch readily to consume non-target prey. They should also be not too bold or exploratory if those BTs tend to disperse outside the target area. In principle, it would be valuable for biocontrol programmes to identify BTs that best balance efficacy of controlling pests while also minimising non-target effects.

## Behavioural correlations

Behavioural correlations across time or across contexts can explain why some individuals or species cope poorly with HIREC. Bold animals remain bold, and cautious animals remain cautious even if these BTs are maladaptive after HIREC. These issues were discussed in the section on how average BTs relate to response to HIREC.

Another role of behavioural correlations involves how HIREC-induced selection for particular BTs can spillover to have correlated effects on behaviour and performance in multiple contexts. For example, consider fishing, Biro *et al.* (2004) suggest that bold individuals are often more likely to be captured. Given that bold fish tend to also be more aggressive and to eat more and grow faster, the remaining unharvested (shy, unaggressive) fish are less likely to outcompete other fish, and less likely to have large impacts on their prey. The harvest-driven shift towards a more shy, unaggressive population could alter sexual selection and social dynamics. This should depend, of course, on capture techniques – e.g. angling vs. seining vs. use of traps vs. passive capture in nets. Similar considerations likely occur with hunting or trapping, including ecological sampling (Biro & Dingemanse 2009). When harvest-restricted zones (reserves) are interspersed with harvest-allowed sites, then BT-dependent dispersal in and out of reserves can also be important in overall dynamics; however, to our knowledge, this issue has not been addressed.

## Within-species variation in BT

Higher within-species variation in BT can facilitate a population's response to environmental change via several mechanisms discussed earlier. Whether or not a species has suitable variation in BT to respond well to HIREC depends on past exposure to evolutionary forces like selection, bottlenecks, drift, gene flow etc. In particular, recent exposure to HIREC could substantially reduce variation in BTs (e.g. via strong selection, or bottlenecks) that could, in turn, reduce ability to respond to ongoing change. To mediate the negative impacts of reduced BT variation, conservation/reintroduction programmes can engage in 'phenotype management' (cf Watters & Meehan 2007) by manipulating environments to increase variation in BTs. For example, habitat restoration, reintroduction or captive rearing programmes might aim to increase variation in habitat structure (or feeding regimes) to facilitate the development and maintenance of greater variation in BTs that can enhance overall population success (Watters & Meehan 2007).

For habitat fragmentation, most studies have emphasised the ecological effects of reduced movement among sites per se. Here, we emphasise that with BT-dependent dispersal (dispersers often tend to be bolder, more exploratory, less social, or more aggressive individuals), the process of dispersal tends to reduce variation in BTs in newly colonised sites (Cote *et al.* 2010a,b). If the reduced variation decreases colonisation success, then the benefit of facilitated dispersal (e.g. via better, safer corridors) is not only to increase movement among patches per se, but also to enhance the movement of BTs that otherwise would be unlikely to disperse.

## ECOLOGICAL INVASIONS

Because invasive species have major, mostly negative ecological and economic impacts (Pimentel *et al.* 2009), understanding species traits

and ecological conditions that allow invasions to occur is a key issue in modern ecology. To be an invasive pest, a species must be successful in all three stages of the invasion process: (1) dispersal and spread; (2) initial establishment in new sites; and (3) growth to large population size and high impact at these sites. Behaviour can be a key trait for explaining success in each of these stages (Holway & Suarez 1999). In particular, recent studies show how behavioural syndromes can provide novel insights on invasion success.

### The species' average BT

Because initial establishment in new sites often requires invaders to cope with new challenges, an intuitively reasonable idea is that successful invaders should be flexible generalists. Support for this hypothesis comes from large, phylogenetically corrected, comparative surveys (Sol *et al.* 2002) showing that taxa that exhibit innovative behaviours (in particular, foraging innovations) are more likely to be invasive around the world. More detailed work on a few species suggests that innovative species tend to have an exploratory BT, and to be good problem solvers perhaps because they have large brain regions associated with problem solving (Lefebvre *et al.* 2004). After initial establishment, high impact, invasive pests tend to be highly aggressive (thus outcompeting native competitors; Duckworth & Badyaev 2007); and/or active foragers (thus likely to have large impacts on native prey (Rehage *et al.* 2005).

### Behavioural correlations and behavioural-type dependent dispersal

Invasion success seems to require different behavioural traits in the different invasion stages. In stage 1 (dispersal), invasive species need to have high dispersal tendency. Initial establishment (stage 2) might require high foraging activity at low density, and the boldness to forage actively even in a novel environment, while having large impacts at high density (in stage 3) might be associated with high aggressiveness even at high density. A positive behavioural correlation between dispersal tendency, foraging activity, boldness and aggressiveness can generate positive correlations between successes in the three stages. Species that are active, bold and aggressive and tend to disperse readily might be 'superspecies' that succeed in all three stages and thus become invasive pests. Although high aggressiveness should tend to help invasive species outcompete native species, high aggressiveness towards conspecifics should make it difficult for an invasive species to grow to high density or to have large per capita impacts on prey. This 'paradox of aggressiveness' (Pintor *et al.* 2009) can be solved, in part, by a positive correlation between aggressiveness and foraging activity. Highly aggressive individuals maintain high foraging activity and thus high foraging rates (Pintor *et al.* 2009) despite frequent aggressive interactions, even at high density.

Correlations between BT and dispersal can generate the aforementioned, BT-based ecological founder effect where new colonists have different BTs than non-invaders of the same species. The fact that dispersers often tend to be the more bold/aggressive individuals from their source habitat (guppies: Fraser *et al.* 2001; great tits: Dingemanse *et al.* 2003; humans: Whybrow 2005; bluebirds: Duckworth & Badyaev 2007; spiders: Riechert & Jones 2008) is an alternative hypothesis to the usual idea that higher aggressiveness in an invaded range is due to

either behavioural plasticity (Sol *et al.* 2002) or evolution of increased aggressiveness associated with release from enemies in the invaded range. If high aggressiveness is a key trait that allows invaders to outcompete and have large impacts on others, then BT-dependent dispersal can be a key mechanism explaining invasion success and impact.

Duckworth & Badyaev (2007) documented the role of BT-dependent dispersal in the range expansion of western bluebirds. The fact that dispersers tend to be highly aggressive helps explain their success in displacing mountain bluebirds (Duckworth & Badyaev 2007). However, after establishing and growing to high density, because aggressive male bluebirds are poor parents, selection favours the evolution of lower aggressiveness behind the invasion front (Duckworth 2008). Whybrow (2005) suggested a parallel BT-dependent dispersal hypothesis for explaining the American cultural psyche which he characterises as greedy and over-consumptive (large ecological footprint, obese). Part of the explanation for the American psyche might be that America has been repeatedly colonised by bold, aggressive, fortune-seekers from other nations.

Individuals that disperse are not always more active, bold or aggressive than non-dispersers (residents). In the above examples, colonists tended to disperse voluntarily. In other cases, dispersers might be subordinate individuals forced out by dominant individuals. In that case, dispersers might have a less aggressive-bold BT than residents. Similarly, in some systems with predation risk-induced dispersal, bold-aggressive individuals might ignore predators and stay, while fearful-unaggressive individuals disperse (Cote *et al.* 2010a). New colonists might then be good at hiding from danger in invaded sites, but would be less likely to be high impact pests.

In several species, within-species variation in dispersal is correlated with sociability (Cote & Clobert 2007; Blumstein *et al.* 2009); e.g. in invasive mosquitofish, dispersers tend to be relatively asocial (Cote *et al.* 2010b). Dynamics are particularly interesting when both dispersal and performance (fitness) depend on an interaction between BT and ecological context, here, density. For example, in the common lizard, at low density, social individuals fare poorly and thus tend to disperse (presumably seeking sites with larger groups to join), whereas at higher density, asocial individuals do poorly and thus disperse seeking low density habitat (Cote & Clobert 2007; Cote *et al.* 2008). Overall, understanding both context and BT-dependent dispersal can be important for understanding BT founder effects that potentially have critical effects on invasion dynamics.

### Within-species variation in BT

The scenario of context and BT-dependent performance and dispersal outlined above suggests that it could be difficult for any single BT to be a successful invasive pest. Asocial individuals colonise empty patches well, but tend to disperse rather than build up to be high density pests; i.e. they are good at stage 2 of the invasion process, but poor at stage 3. In contrast, social individuals attain high densities and have large ecological impacts, but are unlikely to settle and do well in empty patches (particularly if they suffer from an Allee effect in low density patches); i.e. they can be good at stage 3, but not stage 2. A successful invasion with repeated cycles of dispersal, colonisation of empty patches and population growth to high density with high impacts might thus require a mix of BTs. Fogarty *et al.* (2011) modelled invasions involving a mix of both social and asocial BTs. Asocial individuals leave established, high density patches and readily



**Table 1** Effects of behavioural syndromes on ecological processes

	Average species BT	Variation within species in BT	Behavioural correlations
Limits to distribution and abundance	Limited plasticity affects ability to cope with ecological pressures, and thus distribution and success	Variation in BT allows the species to cope with a broader range of environmental conditions and increases long-term success Keystone individuals can have strong impacts on population success, e.g. through the spread of information/innovations (positive impact) or disease (negative impact) Individuals with different BTs have complementary roles with positive synergistic effects	Correlations across situations limits species abilities to cope with different situations, impacting its distribution Correlations among ecologically relevant behaviours can limit population success as selection on a given behaviour will affect correlated behaviours
Species Interactions	BT can affect the intensity of species interactions (e.g. bold/aggressive species having stronger impacts on their competitors and prey) BTs can bias interactions towards particular predator, prey, competitor, or parasite, species Species interactions (nature and strength) can depend on the interaction between the BTs of both species (e.g. performance of predator BTs depend on prey BT and <i>vice versa</i> )	Increased intraspecific variation in BTs variation results in higher functional diversity per species	Trade-offs between behaviours can be a fundamental mechanism maintaining biodiversity  The correlation between BT and dispersal can impact species interactions in post-dispersal habitats
Population dynamics	Species with fast pace-of-life syndromes have more cyclic or stochastic population dynamics Density-dependent regulation of populations are commonly shaped by BTs (e.g. by aggressiveness or sociability)	BT variation may alter the strength of density-dependence if different BTs specialise on different densities BT variation may affect the strength of cycling by introducing time lagged shifts in the relative frequencies of BTs in the population	Behavioural correlations across time can increase time lags inducing cyclic or chaotic dynamics Behavioural correlations can affect the strength of density-dependence due to increased interaction frequency between aggressive BTs BT-dependent dispersal may allow both higher colonisation success and lower extinction rate in metapopulations
Response to novel environment and environmental change	Species that are more exploratory and flexible are typically more innovative and perform better in novel ecological situations (e.g. invasion, urbanisation) Cautious species are more susceptible to human disturbance and more likely to exhibit declining population sizes, but boldness can be detrimental if novel environments are too dangerous Biological control agents need to be flexible enough to cope with novel habitats, but not so flexible to switch readily to consume non-target prey	Higher within-species variation in BT can facilitate a population's response to environmental change  Recent exposure to HIREC could substantially reduce variation in BTs that could, in turn, reduce the ability of populations to respond to ongoing change	Behavioural carryover can limit animals' ability to cope with rapidly changing environments  HIREC can select for particular BTs that spillover to have correlated effects on behaviour and performance in multiple contexts
Ecological invasions	Successful invaders should be flexible generalists because initial establishment in new sites often requires invaders to cope with new challenges and exploit new opportunities BT (e.g. boldness, aggressiveness) influence ability to establish and have high impacts	A mix of BTs can result in an invasion that is both more rapid and builds up to higher densities because within-species variation in BTs expands the range of conditions where a species can be successful	BT-dependent dispersal can generate BT-based ecological founder effects where new colonists have a consistently different BT than non-invaders of the same species  Positive correlations among behaviours can help explain the success of 'superspecies' that do well in all stages of the invasion process

colonise empty patches. Their presence in newly occupied patches facilitates social individuals joining in large numbers. High density then drives out asocial individuals who colonise subsequent empty patches. The mix of BTs can thus produce faster, higher impact invasions than possible with only one BT. Future work should expand the range of BT axes (e.g. include boldness or aggressiveness) and ecological factors (e.g. include competition or predation) in analyses of

how the blend of context and BT-dependent fitness and dispersal might influence invasion dynamics.

## CONCLUDING REMARKS

Although it is clear that behavioural syndromes have important ecological implications, to date, few studies have explicitly focused on

these implications. Although many studies on behavioural syndromes look at fitness effects, few have taken the next step of looking at how these fitness effects influence population or community ecology phenomena. Conversely, although ecologists often acknowledge the importance of variation in BT, few have incorporated the study of behavioural syndromes into their research programmes. There is thus a need for both more mathematical models and empirical work, including experiments contrasting ecological patterns for populations differing in mean and variance in BTs. Future work could, in particular, account for greater complexity in both behaviour and ecology – multiple BT axes and multiple species interactions across multiple ecological contexts. Further work on the bridge between behavioural syndromes and ecology should prove rewarding.

## AUTHORSHIP

All authors participated in extensive discussion and literature review before we wrote this paper. Fogarty wrote the first draft of the section on population dynamics. Pruitt wrote the first draft of the section on species interactions. Cote produced the first draft of the Table. Evans wrote the first draft of the abstract. Sih wrote the first draft of the rest of the paper. All authors contributed to revisions.

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