

REVIEWS AND SYNTHESIS

An evolutionary ecology of individual differences

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Abstract

Individuals often differ in what they do. This has been recognised since antiquity. Nevertheless, the ecological and evolutionary significance of such variation is attracting widespread interest, which is burgeoning to an extent that is fragmenting the literature. As a first attempt at synthesis, we focus on individual differences in behaviour within populations that exceed the day-to-day variation in individual behaviour (i.e. behavioural specialisation). Indeed, the factors promoting ecologically relevant behavioural specialisation within natural populations are likely to have far-reaching ecological and evolutionary consequences. We discuss such individual differences from three distinct perspectives: individual niche specialisations, the division of labour within insect societies and animal personality variation. In the process, while recognising that each area has its own unique motivations, we identify a number of opportunities for productive ‘cross-fertilisation’ among the (largely independent) bodies of work. We conclude that a complete understanding of evolutionarily and ecologically relevant individual differences must specify how ecological interactions impact the basic biological process (e.g. Darwinian selection, development and information processing) that underpin the organismal features determining behavioural specialisations. Moreover, there is likely to be co-variation amongst behavioural specialisations. Thus, we sketch the key elements of a general framework for studying the evolutionary ecology of individual differences.

Keywords

Animal personality, behavioural syndrome, division of labour, individuality, niche variation, niche specialisation, reproductive specialisation.

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INTRODUCTION

Individuals of the same species differ. This fact has long been recognised by careful observers of the natural world (e.g. Aristotle 350 BCE; Darwin 1859) and is so completely uncontroversial that many biologists are happy to accept it without much need for further explanation. However, not all among-individual variation can be so easily accounted for. One particularly noteworthy form involves behavioural variation among individuals within populations that exceeds the variation expressed by individuals over time or in different contexts. Fundamentally, this is because behaviour has the potential to be very plastic so the lack of behavioural flexibility this pattern of variation implies catches the eye. Moreover, in many cases, such within-population behavioural variation can exceed differences amongst populations in distinct environments (Bolnick *et al.* 2003; Bell *et al.* 2009; Stamps & Groothuis 2010). Thus, within a given population, individuals may specialise on particular resources or behaviours (e.g. from a range of social, sexual or anti-predatory responses). Such specialisation can be a major driver of biodiversity because, at its heart, speciation is synonymous with reproductive specialisation within lineages (Rundle & Boughman 2010). Moreover, as behavioural change can precede change in gene frequencies (West-Eberhard 2003), the factors promoting behavioural specialisation within populations deserve specific attention. In this article, we

compare and contrast for the first time three interrelated but distinct perspectives that feature heavily in the current literature on ecologically relevant individual differences in behaviour in natural populations. In the process, we hope to generate substantial and novel insights into the causes and consequences of individuality in evolutionary ecology.

INDIVIDUAL BEHAVIOURAL DIFFERENCES: A SYNTHETIC CONCEPTUAL OVERVIEW

Interest in individual differences in behaviour in natural populations is burgeoning, yet it has arisen independently in several different sub-disciplines of organismal biology, resulting in a fragmented literature. The field of ecology has developed a literature on ‘individual (ecological) niche specialisation’; animal behaviour is increasingly documenting ‘behavioural syndromes’ or ‘animal personalities’; and biologists studying social insects have focused on ‘division of labour’ and ‘caste’ within colonies for much of their history. Although these subfields do not encompass all of the interest in individual differences in behaviour in the evolutionary and ecological literature, we focus on them here because they are coming to dominate this literature. Moreover, our treatment departs from other recent discussions of the impact of variation in behaviour on ecological and evolutionary outcomes (e.g. West-Eberhard 2003;

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Gordon 2011) by focussing on a specific class of individual variation: individual behavioural specialisations within populations of the same species. We begin our synthetic conceptual overview by briefly summarising the key features (approaches and major findings) of the three subfields, before highlighting the main distinctions amongst them and suggesting how lessons from each can enhance understanding in the others.

Individual niche specialisation

Strictly speaking, individual niche specialisation can be used to describe any intrapopulation heterogeneity in biotic interactions or response to abiotic conditions. In practice, the terms 'niche variation' and 'individual specialisation' have been used to describe cases of resource use heterogeneity. Ecologists have documented within-population variation in abiotic tolerance (Meyer *et al.* 2009), microhabitat use (Bolnick *et al.* 2009), prey preferences (Estes *et al.* 2003), predation risk (Eklov & Svanback 2006), parasite resistance or tolerance (Ganz & Ebert 2010), mutualism (Heinrich 1979), dispersal (e.g. partial migration; Chapman *et al.* 2011) and exposure to intraspecific or interspecific competition (Svanback & Bolnick 2007). Collectively, these biotic interactions (and abiotic tolerances) are frequently used to define an organism's ecological niche (Chase & Leibold 2003). Phenotypic variation (as manifest behaviourally) among individuals within a single population can cause individuals to participate in different interactions, with different intensities – a phenomenon known as 'intraspecific niche variation', which is sometimes broken down to distinguish the most common sources of variation. First, phenotypic differences between the sexes can generate niche variation, known as 'ecological sexual dimorphism' (e.g. Temeles *et al.* 2000). Second, differences can arise from phenotypic changes during ontogeny, including size, shape and behaviour, known as 'ontogenetic niche shifts' (Polis 1984). Third, some species contain *discrete* readily distinguishable and ecologically divergent morphs known as 'resource polymorphisms' (Ford 1964), analogous to alternative mating polymorphisms seen in a range of species (Schuster 2010). In some cases, these result from developmental plasticity (e.g. some tiger salamander larvae develop cannibalistic phenotypes in response to overcrowding, modulated by kin environment; Hoffman & Pfennig 1999), and in others from different genotypes or both (see, e.g. table 1 in Bolnick *et al.* 2003). Finally, even after accounting for effects of sex, age and discrete morphs, many populations still exhibit substantial niche differences among individuals (Bolnick *et al.* 2003). This residual among-individual variation is known as 'individual niche specialisation'. The word 'specialisation' is used because among-individual niche differences imply that individuals typically use a narrower subset of the niche space occupied by their population as a whole. Thus, individuals are specialised relative to their population. In a similar way, individual differences in social niche specialisation are being increasingly identified (Bergmüller & Taborsky 2010; Reale & Dingemanse 2010). Individual specialisation thus reflects size, behavioural, morphological or physiological variance among individuals arising from a combination of (1) genetic variation, (2) epigenetic effects such as maternal effects, (3) ontogenetic changes in phenotype, (4) divergence due to adaptive phenotypic plasticity and environmental heterogeneity and (5) stochastic developmental effects. Unfortunately, most empirical studies of individual specialisation do not clearly delineate between these sources of variation or their interactions,

usually because this is almost always impossible to do so without a very precise long-term surveys of behaviour (including foraging behaviour in natural settings), or morphological or physiological traits for individuals of known parentage.

Division of labour in insect societies

Behavioural variation among individuals is fundamental in eusocial insect societies. It has two main components: (1) reproductive division of labour between specialist egg-laying (queen) and working (workers) individuals and (2) among the workers themselves, who typically specialise on different tasks for a few days or even their whole lives. Both have been known since antiquity. Aristotle, for example, knew that honey bee colonies had a distinct ruler-bee and that different workers did different tasks: 'They all have their proper work to perform. Some bring flowers, others water, and others polish and erect the cells' (Aristotle 350 BCE). In many species, including the honey bee *Apis mellifera*, the queen and workers have great morphological differences that begin during larval development with female larvae developing into either a queen or a worker depending on rearing conditions. Furthermore, honey bee workers perform a series of tasks as they age, known as age polyethism, starting with cell cleaning and ending with foraging (Winston 1987). Although this sequence is typical, it can be sped up or slowed down by environmental conditions, such that in a colony with only young bees some start foraging at unusually young ages (Robinson 1992). Thus, individual behaviour can differ among workers of different age classes while being consistent in the short term (on a day-to-day basis) for any given individual. In addition, worker honey bees show heritable variation in their tendency to perform specific tasks: for example, the hygienic removal of dead larvae from cells (Rothenbuhler 1964) or the removal of dead bees from the nest (Robinson & Page 1988). Although honey bee workers are all morphologically identical, in some ants and termites the workers vary in both size and shape. In *Atta* leafcutter ants, for example, there may be a lifelong 200-fold difference in body mass, from the smallest workers, which weed the fungus garden, to the largest, which are defenders and have relatively larger heads with powerful jaws. When the workers are of different sizes or shapes, they tend to specialise in particular tasks for their whole adult lives. For example, the eusocial bee *Tetragonisca angustula* has a morphologically distinct soldier caste of larger workers that act as entrance guards. Only 1% of the workers are the larger soldiers, which guard for weeks; in contrast, morphologically unspecialised honey bee guards typically only guard for a day (Gruter *et al.* 2011). In *Pheidole* ants, workers of two distinct body sizes are reared. As in many ants with worker size variation there is allometry, such that the larger workers have relatively larger heads that assist in their primary role as defenders (Wilson 1971). The large-headed soldier workers also have a much smaller behavioural repertoire than small-headed workers (Oster & Wilson 1979).

Animal 'personality' variation

For anyone who spends time watching animals, there is often a strong sense that individuals differ predictably in their behaviour even within an otherwise uniform population of the same species. Indeed, we, as human observers, effortlessly cue in on individuality and individual patterns behaviour, which dominate the human-centred sciences (e.g. McCrae & Costa 1999) where they focus

predominantly on quantifying such variation without putting it into a broader ecological or evolutionary context. Nevertheless, from an evolutionary and ecological perspective, it is becoming increasingly evident that such stable (consistent and correlated) interindividual variation in the absence of obvious demographic and morphological correlates is distributed widely in natural populations across the animal kingdom (Sih *et al.* 2004a; Reale *et al.* 2007; Smith & Blumstein 2008) and is variously referred to as 'animal personality' (Dall *et al.* 2004), 'behavioural syndromes' (Sih *et al.* 2004b), 'temperament' (Reale *et al.* 2007) and 'coping styles' (Koolhaas *et al.* 1999). The consensus seems to be that personality variation is, at minimum, characterised by substantial interindividual behavioural variation within populations, along with relatively low-levels of flexibility by at least some individuals (i.e. correlated behaviour) over time or across contexts. As an example of the latter, three-spined stickleback fish that are more 'bold' towards a predator when they are juveniles grow up to become exceptionally aggressive towards rival males as adults (Huntingford 1976). Such variation has also been well documented in great tits: individuals differ consistently in exploratory behaviour, and birds that slowly and carefully explore their environment are relatively unaggressive, and respond fearfully to novel objects (Verbeek *et al.* 1994). Moreover, some authors have suggested that the limited behavioural flexibility that characterises personality variation might explain apparently maladaptive behaviours such as precopulatory sexual cannibalism (when a female eats a male prior to mating with him). For example, individual female fishing spiders that are voracious foragers as juveniles are more likely to engage in precopulatory sexual cannibalism as adults (Johnson & Sih 2005). While high levels of juvenile voracity towards prey is adaptive, Johnson & Sih (2005) suggested that voracity 'spills over' to cause inappropriate levels of aggression towards potential mates. Widespread evidence of such variation is emerging from recent behavioural ecology research (see Sih *et al.* 2010 for a recent review), prompted by D. S. Wilson's (Wilson 1998) call for an evolutionarily motivated approach to studying behavioural variation of this nature. Indeed, the evolutionary and ecological importance of such variation is only recently being appreciated (Wolf & Weissing 2010; Chapple *et al.* 2012; Sih *et al.* 2012; Wolf & Weissing 2012). Ostensibly individuals are expected to differ merely due to mutation and stochastic influences during development. Nevertheless, the fact that individuals are behaving in a consistently different manner to those they (potentially) interact with suggests that such variation is likely to affect survival and reproduction and will therefore be a target for selection. Indeed, such fitness consequences of animal personality variation are being documented in a wide range of species (Dingemanse & Reale 2005; Smith & Blumstein 2008), in both the lab (e.g. Schuett *et al.* 2011) and field (e.g. Dingemanse *et al.* 2004). For instance, a recent meta-analysis suggested that consistent differences in exploration typically impact adult survival while such variation in aggression typically impacts reproductive success across a range of species (Smith & Blumstein 2008).

Contrasting approaches

It remains clear from the strength and breadth of the research areas outlined above that the study of individual behavioural differences within groups and populations is gaining prominence amongst evolutionary ecologists. Nevertheless, there are substantial differences

in the motivations underpinning the various approaches to studying this class of biological variation. One of the primary motivations for studying niche specialisation is to understand and accurately characterise ecological processes, such as predator-prey interactions and population dynamics. The presumption is that intraspecific variation in interaction strengths or demographic parameters can alter the dynamics of populations or communities (Bolnick *et al.* 2011). This is because individual organisms participate in multifarious ecological interactions in a diverse community of co-occurring species. The nature of these interactions depends on the phenotypes of individual organisms: size, morphology, physiology and behaviour jointly determine foraging rates, microhabitat use, prey preferences, biomechanical capabilities, immune state, and anti-predator and mating strategies. Consequently, phenotypic (behavioural) variation among conspecifics can generate intraspecific variation in the strength and identity of ecological interactions. Indeed, research is moving away from merely documenting whether individual specialisation exists, to testing hypotheses as to when individual specialisation will be more or less pronounced (e.g. Áraujo *et al.* 2007; Svanback & Bolnick 2007; Bolnick *et al.* 2010), and evaluating the community-ecology consequences of individual specialisation (Bolnick *et al.* 2011). For example, field experiments have shown that intraspecific and interspecific competition tend to increase and decrease individual specialisation, respectively (Svanback & Bolnick 2007; Bolnick *et al.* 2010), suggesting that individual specialisation will tend to be more pronounced in species-poor communities (Bolnick *et al.* 2011).

In contrast, questions motivating scientists who study division of labour include how eusociality or altruism (reproductive restraint) can evolve in a Darwinian world and how animal groups (colonies) are integrated to function effectively. Indeed, from an evolutionary perspective, reproductive division of labour between queens and workers and division of labour amongst the workers are generally investigated in the contrasting perspectives of altruism and conflict vs. efficiency and coordination as they present distinct evolutionary puzzles. Reproductive division of labour involves workers sacrificing direct reproduction and so is a genuine Darwinian puzzle. Eusociality has invariably arisen in the context of high kinship (i.e. in lineages that show high levels of reproductive monogamy) in which helpers rear the offspring of close kin, typically their full siblings (Hughes *et al.* 2008). This is as predicted by Hamilton's theory of inclusive fitness (Hamilton 1964a,b). However, in many modern-day species, the highest levels of worker altruism (and reproductive inequality) are caused by social coercion, such as through the policing of worker-laid eggs (e.g. Ratnieks & Helanterä 2009). In contrast, when studying division of labour among the workers, researchers have generally looked for gains to colony efficiency as a result of having workers specialised for different roles or tasks (Oster & Wilson 1979; Helanterä & Ratnieks 2008; Tschinkel 2011; Dornhaus *et al.* 2012), assuming minimal evolutionary conflicts of interest within colonies. Indeed, where social insect ecological interactions have been considered explicitly, the latter approach has led researchers to consider variation amongst colonies ('super-organisms') as of paramount importance (e.g. Gordon *et al.* 2011). Nevertheless, the potential for conflicts of interest within colonies, suggested by the widespread research focus on social insect altruism/conflict, means that the ecological consequences of individual variation in behaviour within colonies are also worth investigating explicitly.

Finally, animal personality researchers are often interested in explaining apparent limited flexibility in individual behaviour among at least some individuals within a population (relative to the range of behaviour expressed across the population). Indeed, one of the main reasons that animal personality variation is attracting a lot of interest from evolutionary ecologists stems from the consistency of individual behaviour at the heart of the phenomenon. If animals show consistent individual behaviour (i.e. individuals differ behaviourally and such differences persist over time or across contexts), they must exhibit limited behavioural flexibility as conditions vary, or in different contexts. This suggests that individuals will not behave in a perfectly (locally) efficient manner in at least some circumstances (Sih *et al.* 2004a, b). Indeed, if such insidious behavioural inefficiencies are a common feature of animal personality variation, it begs the question of how animal personality can persist over evolutionary time, or whether it is a (possibly transient) feature of animal systems resulting from localised constraints on behaviour that pause evolutionary trajectories at local peaks in the adaptive landscape en route to their stable global optima (Hammerstein 1998). Consequently, there has been substantial effort in recent years by evolutionary theorists to account for this class of behavioural variation in an adaptive sense (Dall *et al.* 2004; Wolf *et al.* 2007; Biro & Stamps 2008; Wolf *et al.* 2008; McNamara *et al.* 2009; Royle *et al.* 2010; Schuett *et al.* 2010; Wolf *et al.* 2011).

These different motivations influence the type of questions asked and show that different perspectives can be usefully brought to bear on the problem. Nevertheless, there are features of each approach that can be applied to the others to enhance the goals set by each discipline (Fig. 1).

Lessons from individual niche specialisation

The literature on individual niche specialisation emphasises the feedback loop between ecological interactions and among-individual variation, primarily focusing on food. Experiments have shown that

intraspecific competition increases individual specialisation (Svanback & Bolnick 2007), but also that individual specialisation mitigates the effects of competition (Ingram *et al.* 2011). However, animal personality researchers rarely consider how competition might be the driving force behind individual variation (but see Reale *et al.* 2010; Wolf *et al.* 2011). Moreover, division of labour in animal societies is rarely thought of as being shaped by competition amongst individuals for access to resources (e.g. Does access to resources underpin variation in the degree of reproductive skew within societies?). The ecological niche specialisation literature also shows that there is tremendous variation in diet among individuals within a population, and there are important ecological implications of such intraspecific variation. One of the classic examples of 'individual diet specialisation' is from a close relative of Darwin's finches, the Cocos finch (*Pinaroloxias inornata*). Over a year, individual finches were observed executing one or a few foraging behaviours, whereas the population as a whole exhibited foraging traits spanning essentially the entire range of passerine feeding ecology: some individuals drank nectar, others ate seeds or fruits, while still other individuals specialised on feeding on arboreal insects or terrestrial insects (Werner & Sherry 1987). The behavioural, social or morphological basis of this variation remains unknown. In other organisms, the mechanisms are better understood. In some cases, such as sea otters, feeding specialisation is learned: transmitted from mother to offspring (Estes *et al.* 2003). In others, individual diet differences reflect phenotypic differences in digestive ability (Afik & Karasov 1995), jaw or beak morphology (e.g. Bolnick & Paull 2009), as well as behavioural differences due to social status (Holbrook & Schmitt 1992) or the development of persistent 'search images' (e.g. Lewis 1986). In contrast, foraging behaviour and diet choice rarely make the list of top behavioural traits examined from an animal personality perspective (apart from social foraging tactic use, like producing vs. scrounging, e.g. Morand-Ferron *et al.* 2011), investigators tend to focus more on boldness, aggressiveness, activity, exploration and neophobia (Reale *et al.* 2007). Nevertheless, understanding how such

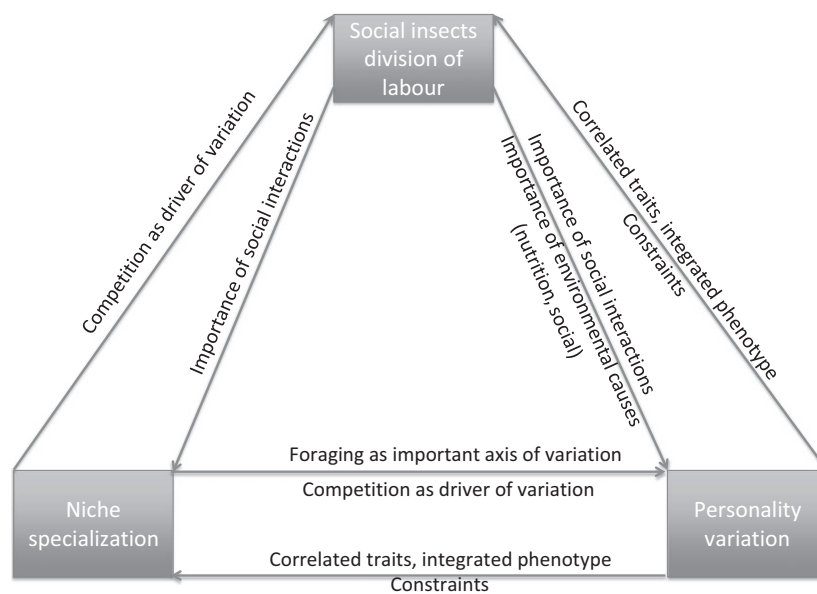


Figure 1 The conceptual links amongst the three different approaches to studying individual differences in behaviour discussed in the text. The diagram summarises the features of each approach that can be applied to the others to enhance the goals set by each discipline.

behavioural variation influences individualised resource acquisition will be crucial to elucidating the fitness consequences of stable behavioural variation (e.g. Dingemans *et al.* 2004; Smith & Blumstein 2008; Schuett *et al.* 2011; Chapple *et al.* 2012; Sih *et al.* 2012). Moreover, the physiological and behavioural processes that underpin resource polymorphisms may help elucidate behavioural variation typically thought of as personality variation (e.g. stable variation in risk-taking behaviour; Wilson & McLaughlin 2010). Such synergy can, in turn, help to broaden the niche specialisation literature to include explicit consideration of individual variation in ecological interactions other than resource use (e.g. predator–prey interactions, reproduction and habitat use).

Lessons from social insect division of labour

The literature on animal societies, and the social insect literature in particular, is too frequently ignored by students of animal personality and niche specialisation. This is likely due to ‘levels of selection’ considerations (Sober & Wilson 2011): for instance, selection might be stronger at the colony level than the individual level, and therefore, processes promoting individual differences within colonies may be qualitatively different from processes promoting individual differences within less structured populations. Nevertheless, it is also likely that evolutionary conflicts of interest amongst individuals within populations will influence selection on patterns of individualised resource access and risk taking, even in relatively unstructured populations. However, there has been very little work to date looking at the influence of relatedness on niche specialisation or animal personality variation (although Royle *et al.* 2010; Schuett *et al.* 2010; Johnstone & Manica 2011 discuss how behavioural consistency can be selected for when such conflicts are minimised – when behavioural coordination is selected for). In fact, the interplay between behavioural coordination and evolutionary conflicts of interest has long interested social insect researchers (e.g. Oster & Wilson 1979; Bourke 1999). For instance, Oster & Wilson (1979) showed how the two dominant perspectives in the social insect literature (altruism/conflict and efficiency/coordination) may interact. Indeed, they demonstrated that ant genera with fully sterile workers (in most eusocial Hymenoptera the workers retain ovaries and can lay unfertilised, male eggs) show a greater tendency to have morphologically distinct worker castes, such as the small-headed and large-headed *Pheidole*, a genus with sterile workers. Does retention of ovaries by workers somehow constrain the evolution of greater morphological variation and division of labour (behavioural specialisation)? Perhaps, in evolving body size variation, workers must also sacrifice some measure of direct reproduction (Ratnieks *et al.* 2011). In addition, in many clades of eusocial Hymenoptera, including honey bees and leafcutter ants, colonies now have reduced kinship due to the evolution of polyandry by queens. Because this evolved not just after the origin of eusociality but after the subsequent evolution of a morphologically distinct worker caste, workers could not opt out of a social life that now provided them with reduced indirect benefits (Hughes *et al.* 2008). In the many groups of eusocial Hymenoptera in which workers and queens are not morphologically distinct, the workers can take over the queen’s role or found a nest. In these single mating prevails.

From a proximate perspective, the social insect literature also provides detailed understanding of how environmental and social influences on behaviour, especially mediated by nutrition, can produce conditional, non-genetic individualised lifestyles (often

underpinned by substantial morphological specialisation) that are irreversible and have substantial consequences for individual reproductive potential (e.g. Ament *et al.* 2008; Kucharski *et al.* 2008). In other words, good examples of how non-genetically based, stable individual differences in behaviour can develop have already been studied in considerable detail. For instance, in the honey bee, it has been known for many years that development into the queen is triggered by royal jelly, the special food secreted by worker bees and fed to larvae being reared in royal cells. Indeed, the identity of the causal ingredient in royal jelly has recently been identified, a polypeptide dubbed Royalactin (Kamakura 2011). In contrast, for most ecological specialisations or animal personality differences, we do not know much about their proximate underpinnings: whether they are driven by genetic variation, epigenetic effects, stochastic environmental effects, developmental plasticity etc. (Stamps & Groothuis 2010). Furthermore, the importance of interactions with conspecifics on the generation and maintenance of individual differences has been studied in the context of competition and niche breadth (Svanback & Bolnick 2007), has been implicit in previous game theoretical treatments of individual differences in the context of alternative mating strategies (Schuster 2010), and is starting to attract attention in animal personality studies (Dall *et al.* 2004; Wolf *et al.* 2008; McNamara *et al.* 2009; Bergmüller & Taborsky 2010; Wolf *et al.* 2011). However, the social insect literature is ripe with well-studied examples of the influence of the social environment on the form and timing of individual specialisations; individuals have specialised *social* roles within the colony, and the cues regulating the development of specialisation are often *social* (see also Arnold *et al.* 2005; English *et al.* 2010 for such examples from vertebrate societies). Therefore, fruitful interchange with the literature on animal societies will be vital as we move towards a more general understanding of stable individuality, both from the perspective of the constraints acting on its evolution (Sih *et al.* 2004a) and how it develops (Stamps & Groothuis 2010).

Lessons from animal personality

One of the key insights that animal personality research offers this discussion is the proposition that individual differences in behaviour are likely to be correlated across functional contexts (e.g. foraging and mating). In general, the existence of such ‘behavioural syndromes’ means that, to understand behaviour in one context, we need to consider behaviour in other functionally important contexts, because how an individual cares for its young might be influenced by how it responds to predators or mates, for example. Similarly, individuals that specialise on eating certain types of food, or that are specialised for a particular task within the colony, might also differ in other important respects. Presumably, a specialised forager not only eats a particular type of food but is also susceptible to different predators and parasites and explores a different habitat while foraging, etc. compared with a forager that is specialised on a different prey type. This perspective also raises interesting questions about the development of individual differences – what is driving what? Presumably, individual differences that arise early in ontogeny can have cascading effects on the entire phenotype. Because individual differences in diet can arise very early during in ontogeny (Garduno-Paz & Adams 2010), diet specialisation is a good candidate process for setting an individual on a trajectory (e.g. Arnold *et al.* 2007) with ramifications for a wide range of other behaviours as it is such a critical feature of the organism’s

overall niche. Indeed, such developmental feedback may also offer insights into the socio-ecological conditions under which subtle differences in reproductive potential among individuals (e.g. colony foundresses) can become exacerbated by ‘state-dependent feedback’ (Dall *et al.* 2004) and underpin substantial reproductive skew in animal societies by limiting the ability of helpers to opt out of social life (e.g. English *et al.* 2010).

There is also the possibility that behavioural choices in different contexts can limit or constrain further specialisation in other contexts. Perhaps, one of the most important consequences of current interest in animal personalities is that it has forced behavioural ecologists to confront an implicit notion that behaviour is infinitely flexible until proven otherwise. Again, when forced to think about it, systemic limitations to behavioural responses should not really be surprising as behaviour reflects what is possible for animals given their morphologies and physiologies. In this way, it should be constrained in similar ways to other phenotypic traits. Indeed, this holistic, Tinbergenian perspective (Tinbergen 1963) suggests that behaviour in different contexts (e.g. foraging, mating) should be analysed as a suite of ‘correlated traits’ (e.g. traits that evolve in tandem) in line with other approaches to thinking about the evolution of phenotypic traits in general (e.g. phenotypic integration, Pigliucci & Preston 2004; ‘G-matrix’ evolution, Phillips & Arnold 1989). Moreover, given the possibility that personality variation reflects the widespread action of constraints on behaviour, appreciation of animal personality variation is forcing

students of the evolution and ecology of animal behaviour to consider the role of proximate factors (e.g. hormones, genes and developmental processes) in more depth than is typical of the field (see Duckworth 2010 for a recent discussion).

TOWARDS AN EVOLUTIONARY ECOLOGY OF INDIVIDUAL DIFFERENCES

The ecological and evolutionary roles of behavioural variation among individuals within populations are clearly of broad interest to ecologists and evolutionary biologists. In this article, we have briefly compared and contrasted three areas, where this type of research has largely been pursued in isolation: ecological ‘niche’ specialisation, animal ‘personality’ variation and divisions of labour within animal societies. In the process, while recognising that each area has its own unique motivations, we have identified a number of opportunities for productive ‘cross-fertilisation’ (Fig. 1). Nevertheless, there are also common elements that are worth highlighting as symptomatic of what could be more broadly described as an evolutionary ecology of individual differences (e.g. Fig. 2).

New techniques are leading the way

A salient feature of the uptick in recent interest in the evolutionary ecology of individual differences is that it is being driven by techni-

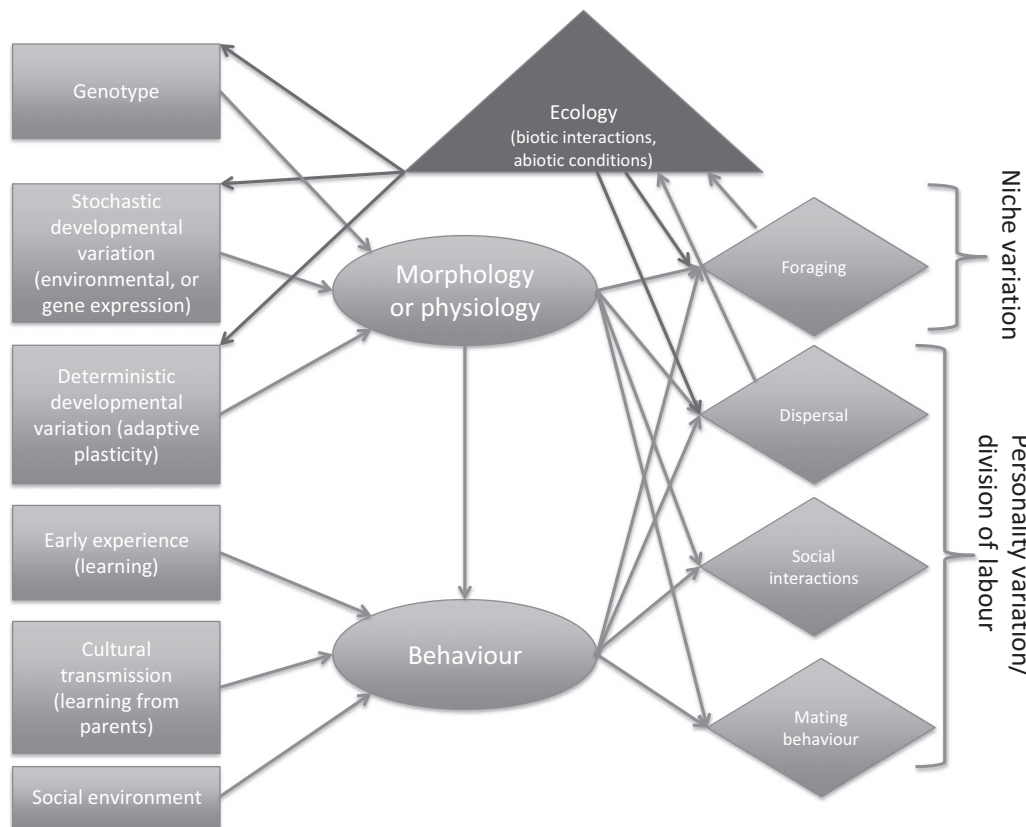


Figure 2 An evolutionary ecology of individual differences. The diagram illustrates how a complete understanding of individual differences must incorporate understanding of how basic biological factors/processes (rectangles: left-hand side) underpin the organismal features (ovals: middle) determining the behavioural specialisations that are the focus an evolutionary ecology of individual differences (kites: right-hand side). Ecological impacts and consequences (triangle) are linked to different levels of the framework, and influence evolutionary processes via links to genotypes. A key feature of this framework is that there is likely to be co-variation amongst the behavioural specialisations and so such links must be investigated explicitly.

cal advances. Much of the burgeoning interest we have highlighted here has stemmed from the emergence of powerful tools for quantifying functionally significant individual variation within groups and populations. These include advances in both data collection techniques to detect previously 'hidden' drivers of stable behavioural variation (e.g. stable isotope analysis, advanced molecular techniques and genomic analysis) and analytical tools for quantifying patterns of individual behaviour within populations (e.g. Bolnick *et al.* 2002; Áraujo *et al.* 2008). Indeed, although interest in ecological genetics (Ford 1964) and resource polymorphisms (Levene 1953) in the mid-20th Century propelled ecological niche specialisations to the forefront of ecological research (Van Valen 1965; Roughgarden 1972), in subsequent decades counter-examples (e.g. Lister 1976) and some theoretical objections (Taper & Case 1985), as well as limited evidence for individual specialisation (e.g. Bryan & Larkin 1972), began to emerge. As a result, the concept was largely abandoned (Grant & Price 1981) although occasional case studies continued to accrue (e.g. Kato *et al.* 2000). Nevertheless, largely as a result of advances in statistical (Bolnick *et al.* 2002; Áraujo *et al.* 2008) and biochemical (Áraujo *et al.* 2007) approaches to measuring individual specialisation, the subject has gained renewed attention (e.g. Bolnick *et al.* 2003; Áraujo *et al.* 2011).

Furthermore, at some level, the study of animal personalities is nothing new. Astute observers of animal behaviour have long noticed that individuals often differ behaviourally (e.g. Aristotle 350 BCE; Darwin 1859). However, although personality in humans has been studied extensively by psychologists (McCrae & Costa 1999) and the importance of correlated traits (including behaviour) has been appreciated by animal breeders (Falconer & Mackay 1996) and evolutionary biologists (e.g. Kruuk 2004) for decades, their insights had rarely been applied to non-human behavioural traits. Nevertheless, in recent years, the study of animal personality variation by evolutionary and behavioural ecologists has started to gather momentum, due in part to advances in techniques for gathering and analysing non-human behavioural data (Dingemanse *et al.* 2010; Stamps & Groothuis 2010). For instance, animal personality researchers are increasingly applying approaches (e.g. 'behavioural reaction norms'; Dingemanse *et al.* 2010) derived from quantitative genetics (Falconer & Mackay 1996; Kruuk 2004) to gathering and analysing detailed data on patterns of individual behaviour. Such approaches enable observed variation in trait expression (e.g. patterns of behaviour) to be statistically partitioned into its constituent influences, including to what degree it is inherited or driven by environmental influences (Falconer & Mackay 1996; Dingemanse *et al.* 2010). This is greatly elucidating the evolutionary significance of personality variation and its links to related phenomena, such as individual behavioural plasticity (Dingemanse *et al.* 2010). However, this type of analysis relies heavily on recent advances in statistical techniques (e.g. random regression; Dingemanse *et al.* 2010), which are often very data hungry and computationally demanding, and have only become widely available to evolutionary ecologists with the modern desktop computer revolution.

Finally, although division of labour within colonies has been studied extensively, recent molecular techniques have greatly enhanced understanding of the mechanisms underpinning such variation. Indeed, worker differentiation presented Darwin a 'special difficulty' to his theory of natural selection (Darwin 1859). The difficulty lay not in explaining the sterility of worker insects, but in explaining how individuals that did not reproduce could themselves be modified by

natural selection, leading to workers that were morphologically distinct from the queens and even, in some ants with polymorphic workers, from each other (Ratnieks *et al.* 2011). This Darwinian quandary spurred substantial research effort, but only recently is work beginning to uncover the underlying molecular mechanisms behind the divisions of labour evident in many systems, including those differentiating queens from workers (Kucharski *et al.* 2008). Moreover, juvenile hormone has long been known to influence age polyethism in honey bees, but recent work is also uncovering additional molecular mechanisms behind this (Ament *et al.* 2008). Thus, the speed of technical advances, along with the pervasive nature of the ecologically and evolutionarily significant interindividual variation they are revealing, offers powerful incentives to continue to investigate such individual variation wherever possible.

'Behavioural specialisation' is key

As well as the technically driven impetus to quantify behavioural variation within populations, there appears to be convergence on the general features of ecologically and evolutionarily 'interesting' interindividual behavioural variation. In all cases, it involves some sort of individual specialisation in behaviour, where behavioural variation among individuals exceeds the degree to which individuals vary the expression of their behaviour over time or across contexts. Such specialisation can be ecologically or socially driven (or both). This suggests an evolutionary ecology of individual differences should focus on broadly inclusive concepts of the individual niche, encompassing both ecological (e.g. Bolnick *et al.* 2003) and social (e.g. Bergmüller & Taborsky 2010) features. While thinking about individual differences as behavioural specialisations is relatively uncontroversial and has a long history in the ecological (e.g. Van Valen 1965; Roughgarden 1972; Bolnick *et al.* 2003) and social insect literatures (e.g. Oster & Wilson 1979; Bourke 1999; Ratnieks *et al.* 2011; Dornhaus *et al.* 2012), ostensibly such a view has not been common amongst animal personality researchers. However, a closer look at the conceptual advances that are driving the current surge in interest in animal personality variation (Wolf & Weissing 2010) suggests that such a perspective is also productive in this context. The key puzzle that recent theoretical explanations for animal personalities have focussed on is how *both* variation amongst individuals within otherwise homogenous groups *and* behavioural consistency/stability over time and/or across contexts can coevolve (Dall *et al.* 2004; Wolf & Weissing 2010). It turns out that all adaptive explanations so far for such coevolution lend themselves naturally to thinking about animal personalities as behavioural specialisations. For instance, a dominant adaptive explanation is that strong life history trade-offs (e.g. between growth and mortality) can select for variation in life history strategies amongst interacting individuals, which can result in individuals following distinct lifestyles with divergent behavioural syndromes (i.e. behavioural specialisations) associated with them (e.g. Wolf *et al.* 2007; Biro & Stamps 2008). Furthermore, even explanations that suggest that differing consistently from others in your group can be selected for directly (e.g. when 'reputation' is at stake: Dall *et al.* 2004; Wolf *et al.* 2011) mean that selection is favouring individuals that specialise socially (Bergmüller & Taborsky 2010).

Characterising individual differences as specialisations that extend across the behavioural phenotype (i.e. that are not just limited to resource specialisations) is likely to have important ecological and evolutionary implications. Indeed, Bolnick *et al.* (2011) review how

intraspecific trait variation changes the outcome of ecological interactions. Many of the examples they discuss involve behavioural traits, and we recommend their framework for considering the direct (ecological) and indirect (eco-evolutionary) consequences of variation within populations. Furthermore, adopting a 'correlated traits' view of the behavioural phenotype as a whole suggests a central role for individual differences in determining the evolutionary dynamics of behaviour (Wolf & Weissing 2012). On the one hand, the interrelated nature of the behavioural phenotype suggested by individual specialisation indicates that simple global optima of the sort typically envisaged by theoretical evolutionary biologists (particularly behavioural ecologists) may not be realistic evolutionary outcomes. Instead, more complex adaptive landscapes are going to have to be considered. Indeed, when the impact of interactions between traits on fitness surfaces have been analysed formally, landscapes go from smooth surfaces with single global peaks (when there are no interactions) to landscapes with a very large number of widely dispersed peaks, but each peak is quite small, as traits interact with each other more and more to determine fitness (Kauffman 1993). In general then, such work suggests that the correlated nature of behavioural phenotypes being revealed by researchers in the fields highlighted here is likely to result in complex behavioural fitness landscapes arising from nonlinear relationships between components of each behavioural trait and interactions amongst such traits (Gilchrist & Kingslover 2001). Such behavioural specialisation-driven landscapes mean that fully characterised evolutionary accounts of behavioural evolution will often require approaches that are not only limited to pure optimisation and game theory considerations but also include the details of the composite trait interactions and their inheritance (Gilchrist & Kingslover 2001).

Phenomenological not mechanistic

By highlighting individual specialisation, it also remains clear that we should avoid restricting ourselves to only studying interindividual variation that is generated by any specific proximate mechanisms (e.g. coded for genetically), thus avoiding potential confusion over levels of explanation (Tinbergen 1963) by focussing on observable patterns of behaviour *per se*. In this way, we feel that an evolutionary ecology of individual differences can encompass variation that is genetically driven, while also considering interindividual variation that involves substantial developmental and behavioural plasticity, and need not be stable for a lifetime but is affected by factors such as social status or condition. This helps to maintain a 'big tent' approach, which will allow further insights to be drawn from considering as wide a range of phenomena as possible from a similar perspective. Indeed, such a stance has the advantage of allowing for further 'cross-fertilisation' with research on other types of intraspecific variation (e.g. colour polymorphisms: Roulin 2004; or alternative mating strategies: Schuster 2010), which is beyond the scope of this study. Nevertheless, an evolutionary ecology of individual differences will ultimately have to involve detailing the mechanisms underpinning the individual behavioural specialisations at its heart to fully understand their evolutionary and ecological consequences, in part because the heritability of trait variance can influence how that variance affects ecological dynamics (Bolnick *et al.* 2011; Sih *et al.* 2012; Wolf & Weissing 2012).

We hope that our synthetic conceptual overview of the fragmented literature on individual differences in behaviour has illustrated the importance of explicitly considering such variation within populations

in all its forms from a common perspective. In the process, we have highlighted a few features that might characterise such a framework (e.g. Fig. 2). It remains clear that by doing so novel insights into ecological and evolutionary processes will emerge. Thus, our synthesis is in keeping with the modern imperative to study variation at all biological scales in evolutionary ecology. Could it be that an emergent evolutionary ecology of individual differences will allow organismal biology to finally shake off the last vestiges of the Platonic typological approach to describing the natural world? We hope so. As Darwin himself pointed out: variety is indeed the spice of life!

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AUTHORSHIP

SRXD organised the collaboration and wrote the first draft of the manuscript. The other authors contributed subsections: DIB on niche specialisation, AMB on animal personality variation and FLW on division of labour. All authors contributed substantially to the final synthesis and revisions.

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