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Current Opinion in Insect Science

Integrating animal personality into insect population and community ecology

Andreas P Modlmeier, Carl N Keiser, Colin M Wright, James LL Lichtenstein and Jonathan N Pruitt

Despite the recent surge of interest in the concept of animal personalities, that is, temporally consistent individual differences in behavior, few studies have integrated intraspecific behavioral variation in population or community ecology. Insects and other arthropods provide ideal model systems to study how intraspecific behavioral variation affects phenomena in ecology. This is due to the fact that arthropods not only are highly amenable to experimental manipulation, but they also allow us to answer general ecological questions on multiple scales of biological organization. Herein, we review recent developments and views on how the framework of animal personality could provide a deeper understanding of classic issues in (1) population ecology (e.g., local adaptation, dispersal, and invasion), (2) community ecology (e.g., food webs and ecosystem engineering), and (3) more insect-focused topics such as metamorphosis and pollination biology.

Address
University of Pittsburgh, Department of Biological Sciences, 4249 Fifth Avenue, Pittsburgh, PA 15260, United States

Corresponding author: Pruitt, Jonathan N (Agelenopsis@gmail.com)

Current Opinion in Insect Science 2015, **9**:77–85

This review comes from a themed issue on **Behavioural ecology**

Edited by **Jacintha Ellers** and **Cécile Le Lann**

For a complete overview see the Issue and the Editorial

Available online 7th April 2015

http://dx.doi.org/10.1016/j.cois.2015.03.008

2214-5745/Published by Elsevier Inc.

Introduction

The past decade has seen a meteoric rise in the number of studies devoted to exploring animal personality. Here we define *personality* as temporally consistent individual differences in behavior along one or more behavioral axes. We define behavioral correlations across ecological contexts as *behavioral syndromes*, and we refer to individuals' phenotypes along these axes as *behavioral types* (BTs). Contexts of behavior may include things like foraging behavior, anti-predator behavior, or mating behavior. Thus, individuals that are more aggressive during foraging might be bolder toward predators or more aggressive toward mates, and so on. Standard axes of behavioral variation considered in this literature include activity level, exploratory behavior, boldness toward predators, aggressiveness toward rivals or food, and sociability [1••].

In general, the animal personality literature describes three mechanisms by which personality can influence ecology. First, the *average* behavioral type of individuals within a population can impact ecological processes. Second, the *degree of variation*, or '*variability*', within individuals (individual consistency vs. flexibility) or among individuals within groups/population (i.e., their behavioral variation) can have pronounced impacts. Finally, third, the intensity and direction of *correlations* among behavioral traits (i.e., syndrome structures) can have subtle, often counterintuitive effects on population and community ecology [2]. In this manuscript we broach various aspects of the population and community ecology of insects and describe ways in which these three aspects of animal personality could enrich these fields. By and large, this paper represents an ideas and perspectives piece, because, to date, there has been very little research on the ecological consequences of animal personality in general. And, insects are no exception to this rule. However, as we discuss below, insects and other terrestrial arthropods have enormous experimental potential relative to vertebrate models, which poises insects to make vibrant and substantive contributions to our understanding of animal personality and its interface with general ecology.

In the sections that follow, we first review instances where animal personality studies on insects have already enjoyed great successes (Section 'Insects: sexual interactions and societies'). This section demonstrates the power of insects as models for personality research, despite their relatively modest presentation within the literature. We then launch into how an animal personality framework can be used to inform issues in the population (Section 'Issues in population ecology') and community ecology (Section 'Issues in community ecology') of insects. Finally, we close by focusing on a small number of issues in insect organismal biology, ecosystem and applied ecology where animal personality could have pronounced effects (Section 'Insects, ecosystems, and applied ecology'). We close each section by summarizing how individuals' *average* behavioral type, the degree of behavioral *variability* within the group/population, and cross-contextual *correlations* in behavior could influence each of these topics.

Insects: sexual interactions and societies

Sexual conflict

The reproductive interests of males and females are often at odds, which can lead to a series of adaptations and counter-adaptations where one sex thwarts the opposing sex for selfish gain. Animal personality can impact the intensity and nature of these interactions, and its application to this literature has yielded much empirical inquiry and conceptual debate [3–5]. For instance, the likelihood that female spiders will engage in precopulatory sexual cannibalism, an extreme instance of sexual conflict, is often mediated by the *average* behavioral tendencies of females [3], where more aggressive females are more likely to kill their mates precopula. In extreme cases, females are so aggressive that they kill all of their would-be mates precopula and die virgins. This phenomenon can be explained because extreme aggressiveness, while costly for mating, improves females' performance during foraging and territory acquisition [3]. The *average* personality types of males can also influence these interactions, where the susceptibility of males depends on subtle interactions between their personality type, body size, and the personality type of the female. Depending on the system, this can lead to both assortative or disassortative mating systems [6,7]. In water striders, hyperaggressive males lock-down entire mating pool, driving females off of the water and effectively sterilizing whole groups of individuals for indefinite periods. With increased behavioral *variability* within pools, a higher proportion of males exhibit this hyperaggressive phenotype and more females disperse. In this system, the entire mating system changes as a consequence of group composition and the presence of one or a few behavioral types [8,9].

As one can see from personality research on spiders and water striders, individuals' *average* phenotype can impact the intensity of sexual conflict between mating partners, and *correlations* between mating behavior and other aspects of behavior may generate cross-contextual performance trade-offs that prevent individuals from deploying optimal behavior in any given context. In striders, the degree of behavioral *variability* within a pool has the potential to dramatically change the mating system of these animals and skew operational sex ratios to extreme male-bias. We argue that the spectacular diversity of mating behaviors deployed by these and other insects (or arthropods) provides a diverse palate from which interested researchers can draw inspiration for further studies.

Social organization

Individuals' behavioral types and the mixture of behavioral types within societies can profoundly impact task participation, social organization, and colony success. While the classic literature on social organization in insects focused on the formation of castes and adaptive caste ratios, recent studies have applied classic theories regarding caste ratios to animal personality (e.g. [10,11]). The striking take-home message from this incipient literature is that animal personality seems to closely match predictions derived from classic theory on morphological castes. For instance, studies have shown that personality shapes the tasks that individuals perform within a colony [12,13], the propensity to switch between tasks [11], and individuals' aptitudes for various tasks [10]. At the colony level, differences in colony composition impact collective behavior [14–17], colony survival [18,19••], reproductive output [20,21], and local adaptation [22••]. This literature has already enjoyed enormous success, and it adds another important axis of functional variation and complexity to our already rich understanding of how these systems operate.

From this literature, we see a large number of studies devoted to how individuals' *average* behavioral type influences their roles within a group and how behavioral *variability* within societies impacts their collective traits and performance. Yet, comparatively less work has focused on cross-contextual *correlations* and the role they might play in structuring insect societies. If cross-contextual correlations generate trade-offs in individuals efficiencies at different tasks, then composing societies of unlike individuals may enhance colony-wide performance. In essence, animal personality may underlie the 'jack of all trade but ace at none' dynamic that underlies much of the classic theory on eusocial societies. One wonders whether and how animal personality evolves in concert with morphological specialization. We further predict that the magnitude and direction of behavioral correlations could predict the intensity of task specialization versus task sharing within different societies. We would be keen to see phylogenetic work and comparative analyses among species that vary widely in their degree of eusociality (e.g., termites, wasps).

Issues in population ecology

Local adaptation

Behavioral types can be a major determinant of how individuals interact with their environment. It is therefore not surprising that we often observe local adaptation in individuals' *average* behavioral type. For instance, crickets from habitats with high predation pressure display stronger anti-predator behavior, that is, they are less bold, than males from low-predation habitats [23]. Similarly, ant populations are more likely to flee (and not fight) in habitats with increasing social parasite pressure [24]. Interestingly, social arthropods might even exhibit local adaptation in their behavioral group composition, or their degree of behavioral *variability*, that is driven by group selection [22••]. In this case, the ideal personality ratio for groups differs across sites, where the mixtures that beget success at one site doom groups elsewhere. Evidence suggests that social groups can respond to this pressure by evolving the ability to adaptively regulate their compositions toward their site-specific optima. Thus, individual reproductive output and survival are often determined by site-specific interactions between individuals' behavioral types and the environment.

Finally, even the *correlations* between behaviors can be locally adapted. For, instance, exposure to predators can generate correlations between boldness and aggressiveness in ''Threespined Stickleback'' [25]. And, comparisons across multiple populations of solitary spiders suggests that they too exhibit site-specific behavioral correlations, again, potentially as a result of site-specific correlated selection (e.g., via exposure to pesticides) [26,27]. What we are missing now are clear instances of selection driving behavioral correlations in insects, and a functional understanding of why particular trait combinations yield superior performance in different environments. We reason that strong differences in behavioral correlations across populations may even increase immigrant inviability and reduce gene flow across sites, potentially facilitating incipient speciation events. Along these lines, we propose that highly controlled mesocosm studies or experimental evolution projects using insect models could be powerful and tenable approaches to address these topics.

Dispersal, founder effects, invasion

Dispersal is often phenotype-biased with bolder and more exploratory individuals showing a higher dispersal tendency (e.g., firebugs [28]). This could be advantageous for the incipient population if the colonizers have a behavioral type that is conducive to pioneering, or detrimental if colonists' behavioral types are poorly matched to early colonizing conditions (e.g., high boldness under high predation pressure [29•]). Hence, we reason that the behavioral types of founders could have long-lasting transgenerational effects that determine the success or extinction of entire lineages (e.g., social spiders [19••]). While founder effects are known to limit genetic diversity, and thus, evolutionary potential [30], they can also promote rapid evolution [31••] and/or invasion success [32]. For instance, much of the invasion success and competitive capability of Argentine ants is attributed to the loss of intraspecific aggression due to low genetic diversity in their introduced range [32]. Lastly, recent studies emphasize that future research should not only consider propagule number, but also incorporate intraspecific trait variation and behavioral plasticity to accurately predict invasions [33,34•].

We argue that insects provide us with a rare opportunity to explore the interactions between *average* behavioral type, behavioral *variability*, and the colonization and establishment of incipient populations. For instance, one might use seasonal range expansions of crop pests to see whether range expansions are characterized by a particular sequence of behavioral phenotypes. The fact that many species of insects do this every year poises these systems for comparative considerations. And, these days, there may be no more-abundant habitat than agroecosystems. We predict that initial colonist could be more active, exploratory, and bold than subsequent colonists, and/or that individuals' average aggressiveness toward conspecifics should go down throughout the season as population densities rise (Figure 1). If such patterns do emerge, insects are also highly amenable to basic experimental procedures (e.g., common garden experiments) that can assess the relative influence of selection versus plasticity in any observed patterns.

Allee effects, extinction

The Allee effect describes a scenario in which decreased mating opportunities and/or other consequences of low population density lead to population decline and even extinction [35]. It is important to consider animal personality in this context, because certain behavioral types might be less susceptible to extinction at low population sizes than others. For instance, more mobile, active bush crickets were able to prevent an Allee effect under low population density [36]. Conversely, more sedentary and inactive individuals could amplify Allee effects and result in a lower effective population sizes and heightened inbreeding.

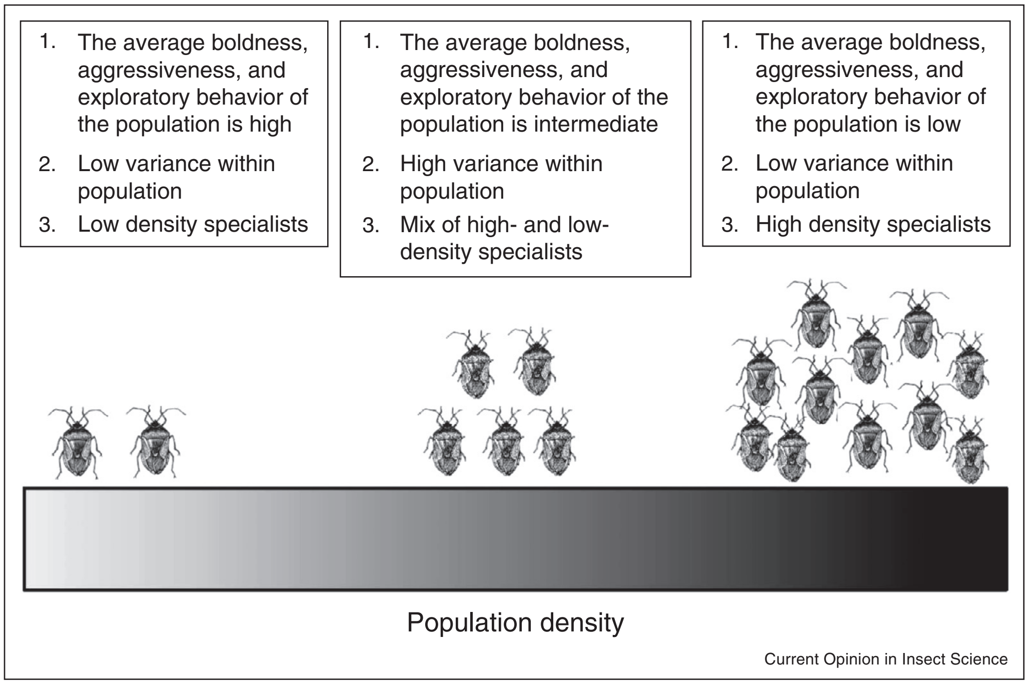
Behavioral *variability* could also influence population connectivity and the strength of Allee effects. As within-population variation in exploration and activity-level increases, there is a greater chance that some dispersal-prone individuals will emerge and beget larger effective neighborhood sizes within populations and enhanced population connectivity. This, in turn, should reduce Allee effects and increase rescue effects in ailing subpopulations (e.g., sink populations). At present, these are merely colorful ideas, but elegant experiments with insect models (e.g., ''mesocosm'' experiments with flour beetles) could transform these ideas into thriving research lines. How behavioral *correlations* of various sorts influence Allee effects and extinction risk is less clear. A modest amount of mental acrobatics could devise numerous predictions. But, here again, arguably some of the only truly viable models for these sorts of topics would be insects and their kin.

Issues in community ecology

Species interactions

In general, intraspecific competition should lead to a stronger individual specialization, while interspecific competition is thought to decrease individual specialization/variation [37]. However, data from a variety of systems, including vertebrates and invertebrates, have shown that animal personality can impact the number of interactions, the intensity of interactions, and the kinds of interactions that individuals have with heterospecifics.

Figure 1



A diagram depicting how the composition of behavioral types within a population might progress as population density increases after colonization.

For instance, individuals with bold, active, or aggressive behavioral types tend to have more dangerous interactions with predators [38,39] and are more susceptible to certain kinds of infectious disease [40]. Likewise, more bold and aggressive individuals are more likely to have diverse diet breadths, which increases the number of species interactions that individuals are involved in. Finally, work on social spiders has shown that individuals' personality types and those of their neighbors (i.e., the behavioral *variability* within colonies) can change the nature of interactions between colonies and their web associates, turning parasites into mutualists or ammenalisms into commensalisms, all as a consequence of animal personality [41••,42].

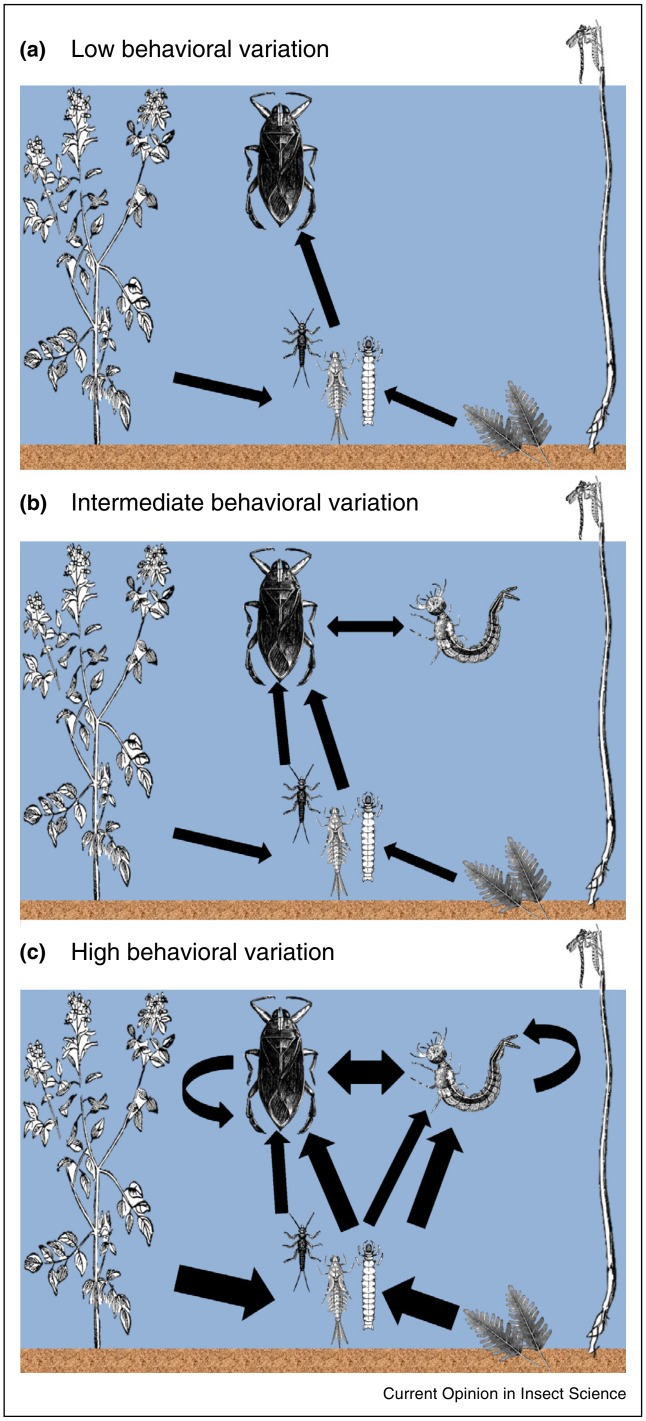
Importantly, the outcome of animal species interactions will also often depend on behavioral type by behavioral type interactions that result in frequency-dependent selection on personality that could maintain behavioral variation. For instance, active predators often primarily consume inactive prey, while sedentary predators tend to consume active prey [43•]. Thus, the profitability of exhibiting any particular personality type in either predator or prey depends on personality types present in the interacting trophic level as well as within their own trophic level. Multi-species frequency-dependent selection has received virtually no attention, despite early indications of its importance in simple ecological modules (e.g., predator–prey interactions) [43•,44]. Here again, insect models have many advantages for these sorts of questions (e.g., experimental tractability, short generation times, large sample sizes, diverse natural history).

In terms of their ability to shape behavioral correlations, we argue that combinations of species interactions are the most likely culprits for driving adaptive behavioral *correlation* structure. For instance, low prey abundance and competition for shelter select for high voracity and intraspecific aggression in the desert spider *Agelenopsis aperta* [45]. Or, high predation and high resource conditions facilitate the emergence of a boldness-aggressiveness syndrome in threespined stickleback [25]. Mesocosm studies that orthogonally manipulate the presence and intensity of various species interactions and note the emergence and disappearance of different *correlation* structures would catapult the literature forward here. Insects, again, seem like the ideal models.

Food webs, trophic cascades, and energy

As discussed above, variation in behavioral types is expected to impact the diversity and intensity of species interactions for any focal species. For instance, highly behaviorally variable species are expected to have more diverse interactions with other species [46]. The community level, an increasing number of diffuse species interactions, coupled with environmental heterogeneity, is, in turn, thought to be conducive for the stability and resilience of communities [47–49] (Figure 2). For instance,

Figure 2



A simplified aquatic food web depicting the predicted trophic structure of communities with increasing behavioral variation within each trophic level. As behavioral variation increases, we expect a greater number of trophic interactions and a more resilient food web. Within each trophic level we predict that bold and aggressive predators will be less discriminatory hunters, attacking a larger swathe of prey types. However, such cases could also result in increased cannibalism or intraguild predation. Communities containing a larger intra-specific and interspecific diversity of behavioral types will be typified by higher energy demands and more rapid energy flow through the system. This, in turn, should have downstream consequences on the emergence time and phenology of hemimetabolous insects, spilling over into terrestrial ecosystems.

predator switching between the most common of two prey behavioral types can result in cycles where total predator and prey density remains stable while densities of alternate prey behavioral types fluctuate [1,50]. Furthermore, since different BTs tend to differ in their ability to persist, invade, and proliferate in novel habitats [34•,47], behavioral variation could conceivably dampen the effects of extreme natural — and anthropogenic — environmental change on population and community-level responses [51]. While all of the above predictions follow from empirical studies (mostly on vertebrates) whether inferences drawn from simplified ecological modules scale to species-rich food webs is again mostly conjecture. Ideally, one would construct experimental food webs and then vary the representation of various behavioral types (or behavioral *variability*) in multiple trophic levels and observe their effects (Figure 2). Obviously, for most study systems, this simply would not be achievable. Yet, with the right insect models, one sees many plausible paths for empirical advancement.

We reason that the *average* behavioral type present within a species (or exhibited by an individual) could also have large impacts on food webs. For instance, we argue that more active, bold and aggressive species (or individuals) will be less discriminatory hunters, attacking larger, more dangerous prey at higher trophic levels [52]. Such cases could result in increased cannibalism [52], intraguild predation [52], or wasteful killing [53], and thus could be typified by high energy demands. Here again, insects have the potential to draw these armchair musing into experimental scrutiny. We argue that this, more than anything else, is what the personality literature needs, and we are not alone in this thinking [54].

Ecosystem services

Certain arthropod personalities may also provide stronger ecosystem engineering services. Ecosystem engineers modify habitats in ways that alter community dynamics and species interactions [55]. Most studies focus on physical alterations to the environment (e.g. termite mounds [56], beaver dams [57], and reef-building corals [58]), though personality alone appears capable of such feats. For instance, the aggressive:docile ratio of the social spider *Anelosimus studiosus* dictates inquiline metacommunity composition, which in turn affects the survival of the whole community [41••]. Community longevity is important because these communities serve as nurseries for an array of arthropod species. Beyond social spiders, insects that make large nests (ants, termites, among others), ant–plant mutualisms, insect gardeners, and species prone to outbreaks are all systems where we believe personality could have large effects on ecosystem services.

Insects, ecosystems, and applied ecology

Metamorphosis

Temporal and contextual carryovers are classic hallmarks of the animal personality literature. As such, insects are fantastic models to test their resulting trade-offs, given their diverse modes of metamorphosis [59••]. While most studies on insect personality focus on hemimetabolous insects with gradual metamorphosis (e.g., crickets [60•]), fewer have directly addressed personality carryovers in animals with contrasting larval and adult stages. For example, Brodin [61] demonstrated that larval personalities carryover to the adult stage in damselflies (but see [62]). Should not the selective pressures operating on larvae differ from that of adults with different ecologies (e.g., aquatic vs. terrestrial, filter feeder vs. predator)? We argue that they should and that this should generate trade-offs as a consequence of individuals' *average* personality type: success at one stage may cost individuals at other stages and vice versa. Thus, no one personality type should experience superior performance across all development stages, and this could facilitate the maintenance of personality variation within populations.

We further query whether the degree of behavior *variability* represented at one developmental stage is accentuated or nullified in subsequent stages. If behavioral variation appears and vanishes from one stage to another, then the behavioral *correlations* across ecological contexts at one stage may be missing from another, as a consequence of reduced variation. Yet, if behavioral correlations are a relatively fixed phenomenon across development, then this too could generate performance trade-offs, because correlated selection at one developmental stage could generate trait associations that prove disadvantageous at other stages. This might all sound vague to the reader because, actually, it is! The personality literature teems with interesting hypotheses but the literature is effectively thwarted by very few (and often middling) experimental assessments. Insects are a plausible remedy.

Pollination

Recent work in honeybees demonstrates a complicated architecture of behavioral, genetic, and social factors influencing a colony's rate and nature of pollen collection (e.g., pollen hoarding syndrome [63•]). However, honeybee personality research has not yet traversed studies on the consequences of pollinator decline. We suggest that universal pollinator loss is likely eroding personality variation in remaining populations. What are the cascading ecological consequences of the loss of variation in pollinator syndromes? Perhaps human-induced rapid environmental changes [51] are inadvertently selecting for more sedentary colonies, causing smaller effective population sizes, increasing the potential for inbreeding, and reducing the area of influence for individual colonies. More basally, the potential links between personality, pollinator efficacy, pollinator choosiness/fidelity, and foraging distance have not been well characterized for any system. This is a wide open field that could have far-reaching implications for animal behavior and general ecology alike. And, nowhere is this research more likely to blossom than in insect model systems.

Pest management

Functional foraging variation in natural enemy assemblages is known to augment biocontrol efforts, though management programs that ignore intraspecific behavioral variation in natural enemies inadvertently neglect this more cryptic variation. Finke [64] demonstrated that greater intraspecific variation in parasitoid specialists fostered greater mortality in aphid communities compared to species diversity *per se*. We reason that similar patterns could emerge elsewhere. Whether behavioral *variability* in multiple control agents accentuates or attenuates the efficacy of their combined control is unclear but, here too, one could devise a series of simple experiments to evaluate these questions in insect models. The pair of studies on this topic both suggest that personality variation can be a major determinant of control potential, at least in generalist predators. Studies on two species of cursorial spider have shown that more active individuals [65] or a mixture of active and inactive individuals [66] are more effective at suppressing pests by 50–80%.

Ecological epidemiology

Individual variation could influence the frequency and severity of disease outbreaks as well. For example, some aphids, the leading vectors of plant pathogens worldwide, exhibit consistent differences in their propensity to drop off of a host plant [67,68••], which is associated with the development of a dispersal polymorphism [69,70]. These 'dropper' phenotypes will produce more disperser offspring, and could transmit viruses more broadly across the landscape relative to non-dropper lineages. There is also expanding theoretical evidence from ant colonies that behavioral diversity decreases the duration of infectious diseases [71], where populations containing diverse BTs are thought to be more resistant to epizootics relative to more homogenous populations. However, certain extreme behavioral types within colonies (high activity/gregariousness/contact rate) may act as 'superspreaders' and their mere presence could prove dangerous for population stability [72•]. These represent mere ideas at this point and their viability awaits more rigorous empirical scrutiny.

Conclusions

The recent integration of intraspecific behavioral variation into classical ecology has resulted in exciting new discoveries in population and community ecology. Given that insects (and other arthropods) are not only highly amenable to experimental manipulation, but also important drivers of ecosystem processes [73], they are well positioned to make empirical advancements that would be difficult or impossible using most vertebrate systems. For instance, much of our understanding of how animal personality guides species interactions is derived from studies involving arthropod models (e.g. [19••,43•,74,75]). This is remarkable considering that the framework of animal personality has only recently been applied to invertebrates (reviewed in [76]), and because few studies (in arthropods or otherwise) have examined the ecological implications of animal personalities [1••]. Yet, we argue that insects and other arthropods should be ideal model systems to study the intersections between population ecology, community ecology and personality, since they provide numerous opportunities to examine not only general ecological issues, but also insect-specific phenomena with far-reaching applied consequences.

Acknowledgements

We want to thank the editors Cecile Le Lann and Jacintha Ellers for inviting us to contribute to this special issue. We are indebted to the editor and two anonymous reviewers for helpful comments on previous versions of our manuscripts. Clipart credits for Figures 1 and 2 go to The Florida Center for Instructional Technology. Funding was provided by the University of Pittsburgh.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. •• Sih A, Cote J, Evans M, Fogarty S, Pruitt J: **Ecological implications of behavioural syndromes**. *Ecol Lett* 2012, **15**:278-289.

This paper surveys the implications if intraspecific behavioral variation and behavioral syndromes influence population ecology, species interactions, population dynamics, anthropogenic climate change, and invasion ecology.

2. Sih A, Bell AM, Johnson JC, Ziemba RE: **Behavioral syndromes: an integrative overview**. *Q Rev Biol* 2004, **79**:241-277.

3. Kralj-Fišer S, Schneider JM, Kuntner M: **Challenging the aggressive spillover hypothesis: is pre-copulatory sexual cannibalism a part of a behavioural syndrome?** *Ethology* 2013, **119**:615-623.

4. Johnson JC: **Debates: challenging a recent challenge to the aggressive spillover hypothesis**. *Ethology* 2013, **119**:811-813.

5. Pruitt JN, Keiser CN: **Debates: the aggressive spillover hypothesis: existing ailments and putative remedies**. *Ethology* 2013, **119**:807-810.

6. Kralj-Fišer S, Mostajo GAS, Preik O, Pekár S, Schneider JM: **Assortative mating by aggressiveness type in orb weaving spiders**. *Behav Ecol* 2013:art030.

7. Pruitt JN, Riechert SE, Harris DJ: **Reproductive consequences of male body mass and aggressiveness depend on females' behavioral types**. *Behav Ecol Sociobiol* 2011, **65**:1957-1966.

8. Sih A, Chang AT, Wey TW: **Effects of behavioural type, social skill and the social environment on male mating success in water striders**. *Anim Behav* 2014, **94**:9-17.

9. Wey TW, Chang AT, Fogarty S, Sih A: **Personalities and presence of hyperaggressive males influence male mating exclusivity and effective mating in stream water striders**. *Behav Ecol Sociobiol* 2014:1-11.

10. Wright CM, Holbrook CT, Pruitt JN: **Animal personality aligns task specialization and task proficiency in a spider society**. *PNAS* 2014, **111**:9533-9537.

11. Holbrook CT, Wright CM, Pruitt JN: **Individual differences in personality and behavioural plasticity facilitate division of labour in social spider colonies**. *Anim Behav* 2014, **97**:177-183.

12. Grinsted L, Pruitt JN, Settepani V, Bilde T: **Individual personalities shape task differentiation in a social spider**. *Proc Roy Soc B* 2013, **280**:20131407.

13. Pamminger T, Foitzik S, Kaufmann KC, Schützler N, Menzel F: **Worker personality and its association with spatially structured division of labor**. *PLoS One* 2014, **9**:e79616.

14. Pruitt JN, Grinsted L, Settepani V: **Linking levels of personality: personalities of the 'average' and 'most extreme' group members predict colony-level personality**. *Anim Behav* 2013, **86**:391-399.

15. Modlmeier AP, Keiser CN, Shearer TA, Pruitt JN: **Species-specific influence of group composition on collective behaviors in ants**. *Behav Ecol Sociobiol* 2014, **68**:1929-1937.

16. Keiser CN, Pruitt JN: **Personality composition is more important than group size in determining collective foraging behaviour in the wild**. *Proc Roy Soc B* 2014, **281**:20141424.

17. Hui A, Pinter-Wollman N: **Individual variation in exploratory behaviour improves speed and accuracy of collective nest selection by Argentine ants**. *Anim Behav* 2014, **93**:261-266.

18. Pruitt JN: **Behavioural traits of colony founders affect the life history of their colonies**. *Ecol Lett* 2012, **15**:1026-1032.

19. •• Pruitt JN: **A real-time eco-evolutionary dead-end strategy is mediated by the traits of lineage progenitors and interactions with colony invaders**. *Ecol Lett* 2013, **16**:879-886.

This study on social spiders demonstrates that the future colonization success of entire lineages depends on an interaction of behavioral group composition (docile:aggressive ratio) of colony founders and inquiline presence.

20. Modlmeier AP, Liebmann JE, Foitzik S: **Diverse societies are more productive: a lesson from ants**. *Proc Roy Soc B* 2012, **279**:2142-2150.

21. Modlmeier AP, Foitzik S: **Productivity increases with variation in aggression among group members in *Temnothorax* ants**. *Behav Ecol* 2011, **22**:1026-1032.

22. •• Pruitt JN, Goodnight CJ: **Site-specific group selection drives locally adapted group compositions**. *Nature* 2014, **514**:359-362.

Using experimentally constituted social spider colonies (*Anelosimus studiosus*) of known behavioral composition, the authors demonstrate that group selection favors site-specific ratios of aggressive to docile individuals.

23. Hedrick AV, Kortet R: **Hiding behaviour in two cricket populations that differ in predation pressure**. *Anim Behav* 2006, **72**:1111-1118.

24. Jongepier E, Kleeberg I, Job S, Foitzik S: **Collective defence portfolios of ant hosts shift with social parasite pressure**. *Proc Roy Soc B* 2014, **281**:20140225.

25. Bell AM, Sih A: **Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*)**. *Ecol Lett* 2007, **10**:828-834.

26. Royauté R, Buddle CM, Vincent C: **Interpopulation variations in behavioral syndromes of a jumping spider from insecticide-treated and insecticide-free orchards**. *Ethology* 2014, **120**:127-139.

27. Sweeney K, Gadd RDH, Hess ZL, McDermott DR, MacDonald L, Cotter P, Armagost F, Chen JZ, Berning AW, DiRienzo N *et al.*: **Assessing the effects of rearing environment, natural selection, and developmental stage on the emergence of a behavioral syndrome**. *Ethology* 2013, **119**:436-447.

28. Gyuris E, Feró O, Tartally A, Barta Z: **Individual behaviour in firebugs (*Pyrrhocoris apterus*)**. *Proc Roy Soc B* 2011, **278**:628-633.

29. • Krams I, Kivleniece I, Kuusik A, Krama T, Freeberg TM, Mänd R, Vrublevska J, Rantala MJ, Mänd M: **Predation selects for low resting metabolic rate and consistent individual differences in anti-predator behavior in a beetle**. *Acta Ethol* 2013, **16**:163-172.
The study on mealworm beetles (*Tenebrio melitor*) links resting metabolic rate with boldness and demonstrates that bolder beetles exhibit a higher mortality under great tit predation.

30. Baker DA, Loxdale HD, Edwards OR: **Genetic variation and founder effects in the parasitoid wasp, *Diaeretiella rapae* (M'intosh) (Hymenoptera: Braconidae: Aphidiidae), affecting its potential as a biological control agent**. *Mol Ecol* 2003, **12**:3303-3311.

31. •• Wessel A, Hoch H, Asche M, von Rintelen T, Stelbrink B, Heck V, Stone FD, Howarth FG: **Founder effects initiated rapid species radiation in Hawaiian cave planthoppers**. *PNAS* 2013, **110**:9391-9396.
The authors' study on Hawaiian cave planthoppers (*Oliarus polyphemus*) supports the concept that founder effects can lead to increased variation in phenotypic traits after founding events presumably via relaxed (sexual) selection. This can shift the phenotype of the founder population once selection resumes with increasing population density.

32. Suarez AV, Tsutsui ND, Holway DA, Case TJ: **Behavioral and genetic differentiation between native and introduced populations of the Argentine ant**. *Biol Invasions* 1999, **1**:43-53.

33. Sagata K, Lester PJ: **Behavioural plasticity associated with propagule size, resources, and the invasion success of the Argentine ant *Linepithema humile***. *J Appl Ecol* 2009, **46**:19-27.

34. • Chapple DG, Simmonds SM, Wong B: **Can behavioral and personality traits influence the success of unintentional species introductions?** *Trends Ecol Evol* 2012, **27**:57-64.
This paper focuses on how behavior and animal personalities can facilitate biological invasions. More specifically, it looks at how personality may be important for the first step on an invasion — introduction into a new habitat. Since most studies begin with staging an invasion, the process of being a stowaway prior to introduction is often overlooked.

35. Courchamp F, Clutton-Brock T, Grenfell B: **Inverse density dependence and the Allee effect**. *Trends Ecol Evol* 1999, **14**:405-410.

36. Kindvall O, Vessby K, Berggren Å, Hartman G: **Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metrioptera roeseli:* an experimental study**. *Oikos* 1998, **81**:449-457.

37. Araújo MS, Bolnick DI, Layman CA: **The ecological causes of individual specialisation**. *Ecol Lett* 2011, **14**:948-958.

38. Storfer A, Sih A: **Gene flow and ineffective antipredator behavior in a stream-breeding salamander**. *Evolution* 1998:558-565.

39. Biro PA, Abrahams MV, Post JR, Parkinson EA: **Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates**. *J Anim Ecol* 2006, **75**:1165-1171.

40. Natoli E, Say L, Cafazzo S, Bonanni R, Schmid M, Pontier D: **Bold attitude makes male urban feral domestic cats more vulnerable to Feline Immunodeficiency Virus**. *Neurosci Biobehav Res* 2005, **29**:151-157.

41. •• Pruitt JN, Cote J, Ferrari MCO: **Behavioural trait variants in a habitat-forming species dictate the nature of its interactions with and among heterospecifics**. *Funct Ecol* 2012, **26**:29-36.
This paper looks at the direct and indirect effects of personality composition in a spider society on species interactions. Specifically, it investigates how personality engineer ecosystems and mediate the community composition and species interactions and how different inquiline compositions can impact colony fitness.

42. Pruitt JN, Ferrari MCO: **Intraspecific trait variants determine the nature of interspecific interactions in a habitat-forming species**. *Ecology* 2011, **92**:1902-1908.

43. • Sweeney K, Cusack B, Armagost F, O'Brien T, Keiser CN, Pruitt JN: **Predator and prey activity levels jointly influence the outcome of long-term foraging bouts**. *Behav Ecol* 2013, **24**:1205-1210.
The authors demonstrate that the outcome of predator–prey interactions between old-field jumping spiders and house crickets depends on the activity levels of both species. Specifically, active jumping spiders have a higher foraging success when they are confronted with inactive crickets and vice versa.

44. Pruitt JN, Stachowicz JJ, Sih A: **Behavioral types of predator and prey jointly determine prey survival: potential implications for the maintenance of within-species behavioral variation**. *Am Nat* 2012, **179**:217-227.

45. Riechert SE, Hall RF: **Local population success in heterogeneous habitats: reciprocal transplant experiments completed on a desert spider**. *J Evol Biol* 2000, **13**:541-550.

46. Bolnick DI, Amarasekare P, Araujo MS, Buerger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA: **Why intraspecific trait variation matters in community ecology**. *Trends Ecol Evol* 2011, **26**:183-192.

47. Cote J, Clobert J, Brodin T, Fogarty S, Sih A: **Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations**. *Philos Trans Roy Soc B* 2010, **365**:4065-4076.

48. Krause J, James R, Croft DP: **Personality in the context of social networks**. *Philos Trans Roy Soc B* 2010, **365**:4099-4106.

49. Pike TW, Samanta M, Lindstrom J, Royle NJ: **Behavioural phenotype affects social interactions in an animal network**. *Proc Roy Soc B* 2008, **275**:2515-2520.

50. Murdoch WW: **Switching in general predators. Experiments on predator specificity and stability of prey populations**. *Ecol Monogr* 1969, **39**:335.

51. Sih A, Ferrari MCO, Harris DJ: **Evolution and behavioural responses to human-induced rapid environmental change**. *Evol Appl* 2011, **4**:367-387.

52. Moya-Larano J: **Genetic variation, predator–prey interactions and food web structure**. *Philos Trans Roy Soc B* 2011, **366**:1425-1437.

53. Pruitt JN, Riechert SE, Jones TC: **Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus***. *Anim Behav* 2008, **76**:871-879.

54. DiRienzo N, Montiglio P-O: **Four ways in which data-free papers on animal personality fail to be impactful**. *Front Ecol Evol* 2015:3.

55. Jones CG, Lawton JH, Shachak M: **Organisms as ecosystem engineers**. *Oikos* 1994, **69**:373-386.

56. Dangerfield JM, McCarthy TS, Ellery WN: **The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer**. *J Trop Ecol* 1998, **14**:507-520.

57. Wright JP, Jones CG, Flecker AS: **An ecosystem engineer, the beaver, increases species richness at the landscape scale**. *Oecologia* 2002, **132**:96-101.

58. Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG: **Ecosystem engineering in space and time**. *Ecol Lett* 2007, **10**:153-164.

59. •• Wilson AD, Krause J: **Metamorphosis and animal personality: a neglected opportunity**. *Trends Ecol Evol* 2012, **27**:529-531.
This review paper explains how animals that undergo metamorphosis (arthropods, marine invertebrates, amphibians) are a neglected but unique set of organisms to study the physiological, morphological, or ecological mechanisms of the maintenance of personality over development.

60. • Hedrick AV, Kortet R: **Sex differences in the repeatability of boldness over metamorphosis**. *Behav Ecol Sociobiol* 2012, **66**:407-412.
This paper demonstrates that boldness was repeatable across metamorphosis in female, but not male field crickets, where males became less bold with maturation, and nymphs in general were bolder than adults.

61. Brodin T: **Behavioral syndrome over the boundaries of life—carryovers from larvae to adult damselfly**. *Behav Ecol* 2009, **20**:30-37.

62. Brodin T, Drotz MK: **Larval behavioral syndrome does not affect emergence behavior in a damselfly (*Lestes congener*)**. *J Ethol* 2011, **29**:107-113.

63. Rueppell O: **The architecture of the pollen hoarding syndrome**
• **in honey bees: implications for understanding social evolution, behavioral syndromes, and selective breeding**. *Apidologie* 2014, **45**:364-374.
This paper describes the complicated architecture of behavioral, genetic, and social factors influencing the rate and nature of pollen collection in honeybee colonies.

64. Finke DL, Snyder WE: **Niche partitioning increases resource exploitation by diverse communities**. *Science* 2008, **321**:1488-1490.

65. Keiser CN, Slyder JB, Carson WP, Pruitt JN: **Individual differences in predators but not producers mediate the magnitude of a trophic cascade**. *Arthropod Plant Interact*, in press.

66. Royaute R, Pruitt JN: **Varying predator personalities generates contrasting prey communities in an agroecosystem**. *Ecology*, provisionally accepted.

67. Schuett W, Dall SR, Baeumer J, Kloesener MH, Nakagawa S, Beinlich F, Eggers T: **Personality variation in a clonal insect: the pea aphid, *Acyrthosiphon pisum***. *Dev Psychobiol* 2011, **53**:631-640.

68. Schuett W, Dall SR, Kloesener MH, Baeumer J, Beinlich F,
•• Eggers T: **Life-history trade-offs mediate 'personality' variation in two colour morphs of the pea aphid, *Acyrthosiphon pisum***. *J Anim Ecol* 2015, **84**:90-101.
This paper shows that red morph ''dropper'' BTs in pea aphids exhibit a risk-averse life-history strategy while red ''nondroppers'' exhibit a risk-prone strategy; life-history strategies were equivalent for all green morph BTs.

69. Weisser WW, Braendle C, Minoretti N: **Predator-induced morphological shift in the pea aphid**. *Proc Roy Soc B* 1999, **266**:1175-1181.

70. Podjasek JO, Bosnjak LM, Brooker DJ, Mondor EB: **Alarm pheromone induces a transgenerational wing polyphenism in the pea aphid, *Acyrthosiphon pisum***. *Can J Zool* 2005, **83**:1138-1141.

71. Naug D, Camazine S: **The role of colony organization on pathogen transmission in social insects**. *J Theor Biol* 2002, **215**:427-439.

72. Modlmeier AP, Keiser CN, Watters JV, Sih A, Pruitt JN: **The**
• **keystone individual concept: an ecological and evolutionary overview**. *Anim Behav* 2014, **89**:53-62.
This review paper outlines the concept of keystone individuals, which have a disproportionally large effect on groups, and proposes methodological approaches to study their ecological and evolutionary impacts.

73. Yang LH, Gratton C: **Insects as drivers of ecosystem processes**. *Curr Opin Insect Sci* 2014, **2**:26-32.

74. Pamminger T, Modlmeier AP, Suette S, Pennings PS, Foitzik S: **Raiders from the sky: slavemaker founding queens select for aggressive host colonies**. *Biol Lett* 2012, **8**:748-750.

75. Keiser CN, Pruitt JN: **Spider aggressiveness determines the bidirectional consequences of host–inquiline interactions**. *Behav Ecol* 2014, **25**:142-151.

76. Kralj-Fišer S, Schuett W: **Studying personality variation in invertebrates: why bother?** *Anim Behav* 2014, **91**:41-52.