Behavioural syndromes and social insects: personality at multiple levels

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ABSTRACT

Animal personalities or behavioural syndromes are consistent and/or correlated behaviours across two or more situations within a population. Social insect biologists have measured consistent individual variation in behaviour within and across colonies for decades. The goal of this review is to illustrate the ways in which both the study of social insects and of behavioural syndromes has overlapped, and to highlight ways in which both fields can move forward through the synergy of knowledge from each. Here we, (*i*) review work to date on behavioural syndromes (though not always referred to as such) in social insects, and discuss mechanisms and fitness effects of maintaining individual behavioural variation within and between colonies; (*ii*) summarise approaches and principles from studies of behavioural syndromes, such as trade-offs, feedback, and statistical methods developed specifically to study behavioural consistencies and correlations, and discuss how they might be applied specifically to the study of social insects; (*iii*) discuss how the study of social insects can enhance our understanding of behavioural syndromes—research in behavioural syndromes is beginning to explore the role of sociality in maintaining or developing behavioural types, and work on social insects can provide new insights in this area; and (*iv*) suggest future directions for study, with an emphasis on examining behavioural types at multiple levels of organisation (genes, individuals, colonies, or groups of individuals).

Key words: behavioral syndromes, behavioural types, levels of organisation, behavioural carryover, behavioural consistency, temperament, repeatability.

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I. INTRODUCTION

In recent years, numerous studies have found that animals exhibit 'personalities' or behavioural syndromes—consistent and/or correlated behaviour across two or more situations (Gosling, 2001; Dall, Houston & McNamara, 2004; Sih, Bell & Johnson, 2004*a*; Sih *et al.*, 2004*b*; Réale *et al.*, 2007; Biro & Stamps, 2008; Sih & Bell, 2008; Dall *et al.*, 2012; Garamszegi & Herczeg, 2012). For example, although most individuals alter their level of aggression depending on the ecological situation (e.g. resource availability or predation risk), some are consistently more aggressive than others (Riechert & Hedrick, 1993; Wilson *et al.*, 1994; Sih, Kats & Maurer, 2003; Duckworth, 2006; Bell & Sih, 2007; Johnson & Sih, 2007). Furthermore, aggressive behaviour is often correlated with bold behaviour or high activity level (Huntingford, 1982; Riechert & Hedrick, 1993; Bell, 2005; Johnson & Sih, 2005). To date, much of the work on behavioural syndromes has focused on variation in boldness, aggressiveness, or activity level (Réale *et al.*, 2007), referred to here as 'classical' behavioural types.

Consistent individual differences in behaviour have long been recognized and studied in several taxa, including humans, primates, laboratory rodents, and a few domesticated mammals (Gosling, 2001). Intraspecific differences in behavioural type have also been described when individuals differ in morphology. This includes classic stereotypical ideas on differences in behavioural type between males and females, and between alternative mating morphs [e.g. larger, aggressive, territorial males *versus* smaller, sneaky, satellite males (Gross & Charnov, 1980)]. Recent studies, however, have emphasized that individual behavioural differences also exist in animal taxa that lack phenotypic polymorphism (Sih *et al.*, 2004*b*).

Social insects can exhibit behavioural variation at multiple levels of organisation: between species, colonies, castes, individuals, and genetic lines (Keller, 1999). Social insect species have long been known to differ in behavioural type (e.g. more aggressive species outcompete and may even displace subordinate species; Davidson, 1998; Holway & Suarez, 1999). Social insect castes (i.e. reproductive or morphologically distinct individuals) also differ in behavioural tendencies often associated with their specialized task (e.g. soldiers are more aggressive than other workers). Thus, social insect researchers have always considered, and quantified, behavioural syndromes. However, until recently, few social insect studies have investigated differences in behavioral type among colonies (within a species) or among monomorphic individuals within a colony (but see Jeanne, 1988). In addition, few social insect studies have investigated whether variation in behavioural type carries over across tasks. For example, in species that exhibit temporal polyethism (workers transition between tasks over time), it would be interesting to determine whether young nurses (brood-care workers) with a highly aggressive behavioural type are also more aggressive as older foragers or more likely to guard the nest. Such consistency in behavioural type carried over across task transitions could have implications for colony fitness.

(1) Defining 'behavioural syndromes'

Behavioural syndromes are defined as consistent individual differences, within a population, in behaviour within and across context (Table 1). If an individual differs consistently in a behaviour (e.g. is consistently more aggressive than others),

Table 1. A comparison of terms used in animal behavior and social insect biology that describe similar phenomena

Animal behaviour terms	Social insect biology terms
Behavioural syndrome	
Individuals within a population exhibit consistency/correlation in two or more functionally different behaviours	
Animal personality	Morphological/reproductive caste
Individuals within a population exhibit consistency in a single behaviour	Physiological constraints (genetics, morphology, hormones, etc.) predispose individuals to perform specific behaviours (e.g. queens and workers)
Behavioural type	Behavioural specialisation
Individual exhibits consistent behaviour across contexts and/or over time. Repeatability or consistency of the magnitude of behaviour often observed. This can be a continuous or discrete variable.	Individual exhibits consistent task performance (that is not necessarily determined by its morphology)
Episodic personality	Temporal polyethism
Response to one set of stimuli predicts the response to other sets of stimuli over a short time scale. Responses are inconsistent over longer time scales.	In a predictable order, individuals switch among tasks as they develop.
	Task switching
	Individuals switch among tasks throughout their lifetime.
Keystone individuals	Elite workers/activators
An individual that significantly alters the behaviour of other individuals within the group.	Individuals that stimulate others, perform multiple tasks, or perform a disproportionate amount of work in the colony.

then that individual has a behavioural type (Table 1), and the population has a behavioural syndrome (Sih *et al.*, 2004*a*; Dingemanse *et al.*, 2010). Recently, Garamszegi & Herczeg (2012) differentiated animal personalities ('consistency in single behaviours') and behavioural syndromes ('consistency in two or more functionally different behaviours') (Table 1). These distinctions are most important when developing experimental design and performing statistical analyses (see Section III.3). In either case, to test whether individuals differ in behaviour in a particular context, it is necessary to quantify the behaviour of a set of individuals in standardized conditions, e.g. while foraging or building a nest (Réale *et al.*, 2007). Although most of the recent interest has been on differences among individuals in behavioural type, one can also look for consistent differences among populations or species in behavioural type. Social insects allow for additional levels of analysis—caste (within colonies) and colony.

(2) Mechanisms affecting behavioural type

A growing literature examines the mechanisms associated with differences among individuals of a behavioural type. Numerous studies have quantified physiological or neuroendocrine correlates of behavioural types (Koolhaas *et al.*, 2007; Biro & Stamps, 2008; Careau *et al.*, 2008; van Oers & Mueller, 2010). Genetic studies show that behavioural types typically exhibit low to moderate heritability (i.e. heritability (H^2) = 0.2–0.5; van Oers *et al.*, 2005; Penke, Denissen & Miller, 2007; van Oers & Mueller, 2010), with recent studies identifying candidate genes, often associated with neuroendocrine pathways, that explain some of the variation among

behavioural types (e.g. Ben-Shahar *et al.*, 2002; van Oers & Mueller, 2010). Genetic effects on behavioural types are also typically moderated by individual experience. In particular, early experience can often have strong effects on the development of a later behavioural type and associated hormonal 'stress response' systems (Stamps & Groothuis, 2010; Del Giudice, Ellis & Shirtcliff, 2011; Sih, 2011). Many of these mechanisms have been studied in social insects; however, as highlighted below, much remains to be discovered.

(3) Fitness effects of behavioural syndromes

Recent behavioural syndrome research has focused on the ecological and evolutionary relevance of within-population variation in behavioural type. An individual's behavioural type can clearly affect its fitness, typically in context-dependent ways (Smith & Blumstein, 2008); e.g. in a safe environment, selection might favour bold individuals that enjoy high feeding or mating success, but in a dangerous environment, cautious individuals might be more likely to survive (Fig. 1A). Notably, if individuals of a particular behavioural type exhibit limited behavioural plasticity, their behaviour could be suboptimal in situations that do not fit their behavioural type well. For example, bolder individuals can be inappropriately bold when predators are present (Sih *et al.*, 2003), and aggressive individuals can be inappropriately aggressive towards mates (Johnson & Sih, 2005), or can exhibit poor parental care (Duckworth, 2006). Given the potentially strong effects of behavioural types on fitness, many studies have asked how variation in behavioural types is maintained, e.g. *via* environmental variation in selection
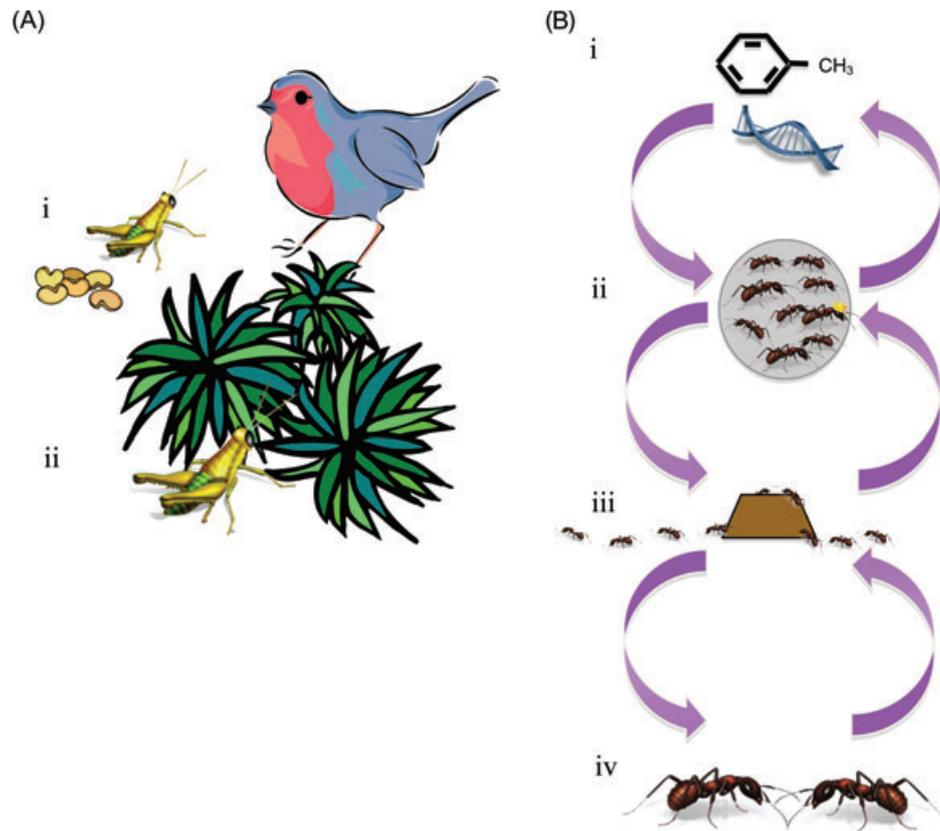
Fig. 1. Concepts that have been borne out in behavioural syndrome (A) and social insect (B) research that could benefit the other field. (A) Behavioural syndromes—trade-offs of behavioural type across ecological context. Trade-offs associated with behavioural syndromes help us understand why populations maintain correlated behavioural types. For example (*i*) a bold cricket will be a better procurer of food, but (*ii*) a shy cricket will be less likely to be seen and eaten by a predator. (B) Social insects—multiple levels of selection/organisation. (*i*) Development of an individual's behavioural type is affected by internal and external mechanisms. (*ii*) Intra-colony composition (variation within and among castes) and development may affect colony behaviour (performance). (*iii*) Colony performance may feedback and influence intra-colony composition. (*iv*) Inter- and intra-colony interactions can feed back and affect colony-level behaviour.

pressures (Dingemanse *et al.*, 2004), frequency dependence (Dall *et al.*, 2004; Pruitt & Riechert, 2009), or condition dependence (Luttbeg & Sih, 2010). Behavioural syndromes can also have important ecological implications, e.g. effects on species interactions, population dynamics, ecological invasions, etc. (Sih *et al.*, 2012).

II. SOCIAL INSECTS AND A HIERARCHY OF BEHAVIOURAL TYPES

Social insects are unique in that selection acts on multiple levels (Fig. 1B; Folse & Roughgarden, 2010). In a social insect colony, workers and queens are individual organisms, but the colony itself can be considered a 'superorganism' (Hölldobler & Wilson, 2009). In general, colonies produce more colonies: the queen as the primary reproductive resembles a 'germ cell', whereas non-reproductive workers resemble 'somatic cells' in that they care for their sisters and queen but do not directly contribute to the next generation. However, in many species,

workers might also compete with one another and the queen to lay unfertilized eggs which can develop into reproductive males. Consistent individual differences (i.e. behavioural types) are found at both levels of organisation: within a colony (among workers and queens), and across colonies. Here we review the current knowledge of individual variation within and among colonies. We discuss both the mechanisms and fitness consequences of variation at each of these two levels.

(1) Variation within colonies

Individuals in social insect colonies commonly differ consistently in behaviour. This is usually interpreted as an effect of their allocation to specialized roles or 'tasks', e.g. nurses, guards, foragers, etc. Such specialization produces a division of labour, and is thought to be adaptive at the colony level (Robinson, 1992; Beshers & Fewell, 2001). When there is variation in morphology (castes; Table 1), such as soldiers *versus* 'minor' workers (Wilson, 1976), behavioural variation might be correlated with caste differences, although variation could also be found within a caste. The majority

of social insect species, however, are monomorphic, i.e. there are no morphological differences between workers (Hölldobler & Wilson, 1990). Nevertheless, workers that look the same might vary greatly in their behaviour. In some cases, these behavioural differences might lead to task groups or behavioural specialisations (Table 1), and still variation can be observed within these behavioural groups. Thus, social insects provide ample opportunities for studying the effects of morphology and other factors on behavioural syndromes.

(a) Variation in morphological castes

Morphological castes are an important functional 'grouping'; variation in morphology often predisposes individuals to behave in a certain manner or to perform particular tasks (Oster & Wilson, 1978; Hölldobler & Wilson, 1990). Even in non-insect social groups, individuals often differ in behavioural tendencies based on morphology (e.g. males and females; Del Giudice, 2011) or body size (e.g. courting *versus* coercive mating tactics in large and small mosquitofish males; Hughes, 1985). In social insects, castes are thought to be a colony-level adaptation (Oster & Wilson, 1978; Hölldobler & Wilson, 1990): morphologically specialized individuals are able to perform functions that would otherwise be inaccessible (e.g. defensive soldier castes in *Cephalotes spp.* ants; Powell, 2008).

Within a caste, a range of behavioural variation might also persist. For example, task preference or efficiency can vary within caste. Within the forager/worker caste of leaf-cutter ants, as mandibles wear away, the individual can no longer cut leaves efficiently and thus perform the function to which this particular morphology predisposes it (Schofield *et al.*, 2011). This wear not only creates variation within the caste in terms of cutting efficiency, but it also prompts a switch in task preference to carrying leaves instead of cutting (Schofield *et al.*, 2011).

To date there has been little work exploring the extent to which individuals within a caste vary in other behaviours (Table 2). For example, are some soldiers more aggressive than others, and are they also aggressive in other situations aside from nest defence? While studies have highlighted the relative importance of castes to colony function (Porter & Jorgensen, 1981; Powell & Franks, 2006; Powell, 2008), little has been done to explore the importance of behavioural variation observed within castes.

(b) Variation in monomorphic species

Variation in behavioural type has also been observed in species without clear morphological castes. In social insects, social behavioural types (e.g. foraging, defence, etc.; Table 2) are the most commonly studied. Still, individuals within a colony could vary in behavioural type along a variety of axes such as those studied in the classic behavioural syndrome literature and/or the cognitive ecology literature (Sih & Del Giudice, 2012; Table 2). For example, *Myrmica spp.* ant workers vary not only in the task they are most likely to perform, but also in general behavioural type: patrollers are bolder, more aggressive, and more exploratory across various contexts than nurses or foragers (Chapman *et al.*, 2011).

In social insect research, a lot is known about how individual workers differ in behaviour in ways that affect their role in the colony, and how these behaviours correlate with others across contexts (i.e. behavioural syndromes). A well-studied case is variation among honey bee (*Apis mellifera*) foragers. Some individuals have lower sucrose response thresholds (i.e. are more likely to respond to less-concentrated nectar), and are more likely to collect pollen, whereas those with higher sucrose response thresholds are more likely to collect nectar while foraging (Page, Erber & Fondrk, 1998; Scheiner, Erber & Page, 1999; Scheiner, Page & Erber, 2004). Sucrose response thresholds also correlate with reproductive development in workers (Amdam & Page, 2010), forager decision-making (Cakmak *et al.*, 2009), the likelihood of collecting non-food rewards, such as water or resin (Simone-Finstrom, Gardner & Spivak, 2010) and learning ability (Scheiner, 2012). In this sense, the cluster of correlated behaviours associated with sucrose response threshold is a broad behavioural syndrome affecting a series of seemingly unrelated behaviours across a variety of contexts.

We also observe variation in behaviours not directly corresponding to particular tasks. For example, although more aggressive workers might be more likely to engage in colony defence (i.e. more likely to attack non-nestmates: Crosland, 1990; Modlmeier & Foitzik, 2011), they could also be inappropriately aggressive to nestmates (van Doorn, 1989; Powell & Tschinkel, 1999; Robson *et al.*, 2000; Foster *et al.*, 2004; Molina & O'Donnell, 2009).

(c) Mechanisms underlying intra-colony variation in behavioural type

(*i*) *Genetics.* Multiple mating by a queen leads to an increase in within-colony genetic variation (i.e. workers are less related to one another) that can result in intra-colony variation in behavioural types (Table 3). In harvester ants (*Pogonomyrmex spp.*), genotype could predispose an individual to develop into a queen or a worker (Volny & Gordon, 2002; Cahan & Keller, 2003; Schwander, Cahan & Keller, 2007; Schwander *et al.*, 2010). Genotypic differences in honey bees might affect individual learning differences (Chandra, Hosler & Smith, 2000) and foraging preferences (Page *et al.*, 1998). Genetic factors are also linked to how quickly a honey bee worker transitions between tasks (Page *et al.*, 1998; Amdam & Page, 2010). Page, Rueppell & Amdam (2012b) have summarized many of these genetic effects in terms of the 'pollen-hoarding syndrome', and have shown how overlapping genetic architecture could provide a mechanism for behavioural syndromes, both at the individual and colony level.

Behavioural variation also readily occurs within colonies where queens only mate with one male, making all workers full sisters and intra-colony genetic variation low [e.g. bumble bees (Jandt & Dornhaus, 2009), rock ants (Dornhaus *et al.*, 2008), social spiders (Pruitt *et al.*, 2011)]. In these cases, gene expression difference might underlie behavioural variation (Table 3). For example, differential expression of the *for*

Table 2. Traits in which individual (= Intra-colony) and colony (= Inter-colony) level behavioural variation, i.e. different behavioural types, have been measured in social insects

	Behavioral type	Intra-colony-level examples	Inter-colony-level examples
Classical	Aggression	Ants Chapman *et al.* (2011), Crosland (1990), Modlmeier & Foitzik (2011) and Powell & Tschinkel (1999) Bees Pearce *et al.* (2001) Wasps Cant *et al.* (2006), Reeve & Nonacs (1997) Termites Adams *et al.* (2007)	Ants Buczkowski & Silverman (2006), Crosland (1990) and Suarez *et al.* (2002) Bees Pearce *et al.* (2001) Termites Adams *et al.* (2007)
	Exploration	Ants Chapman *et al.* (2011) and Modlmeier & Foitzik (2011)	
	Boldness/shyness	Ants Chapman *et al.* (2011)	
	Proactive/reactive		Ants Gordon *et al.* (2011) and Pinter-Wollman *et al.* (2012a)
Cognitive	Sensory bias/preference	Bees Page *et al.* (2012b), Spaethe *et al.* (2007) and Spaethe & Chittka (2003)	Bees Ings *et al.* (2009), Raine & Chittka (2005, 2007b) and Raine *et al.* (2006a)
	Learning	Bees Latshaw & Smith (2005), Laverty (1994), Lihoreau *et al.* (2012b), Molet *et al.* (2009), Muller *et al.* (2010), Page *et al.* (2012b), Raine & Chittka (2012), Scheiner *et al.* (2003) and Worden *et al.* (2005)	Bees Chittka *et al.* (2004), Ings *et al.* (2009), Raine & Chittka (2008, 2012) and Raine *et al.* (2006a,b)
	Speed and accuracy in decision-making	Bees Burns & Dyer (2008), Chittka *et al.* (2003), Dyer & Chittka (2004) and Kulahci *et al.* (2008)	Ants Pinter-Wollman *et al.* (2012a) Bees Wray & Seeley (2011)
Social	Cooperation	Ants Cahan & Fewell (2004) Social Spiders Pruitt & Riechert (2009)	Ants Cahan (2001) Bees Robinson *et al.* (1990) Social Spiders Pruitt & Riechert (2011)
	Communication	Ants Pinter-Wollman *et al.* (2011)	Bees Mattila *et al.* (2008)
	Hygienic behaviour	Ants Diez *et al.* (2011) Bees Arathi *et al.* (2000) and Visscher (1988)	Ants Scharf *et al.* (2012) Bees Paleolog (2009) and Wray *et al.* (2011)
	House-hunting	Ants Pinter-Wollman *et al.* (2012b) Bees Liang *et al.* (2012)	Bees Wray & Seeley (2011)
	Foraging	Ants Beverly *et al.* (2009), Gordon *et al.* (2005) and Pinter-Wollman *et al.* (2012b) Bees Fewell & Page (1993), Liang *et al.* (2012), Lihoreau *et al.* (2010, 2011, 2012a,b), Muller *et al.* (2010), Page *et al.* (2012b), Raine & Chittka (2007a), Robinson & Page (1989), Saleh & Chittka (2007) and Spaethe & Weidenmüller (2002)	Ants Bengston & Dornhaus (2013), Cole *et al.* (2010), Gordon *et al.* (2011), Gordon *et al.* (2013) and Pinter-Wollman *et al.* (2012a) Bees Gill et al. (2012), Ings *et al.* (2006), Page *et al.* (2012b), Raine & Chittka (2007b, 2008) and Wray *et al.* (2011)
	Defense	Bees Grüter *et al.* (2012)	Ants Pinter-Wollman *et al.* (2012a) Bees Wray *et al.* (2011)

We divide these into: 'classical'—those behavioural axes most commonly measured in the behavioural syndrome literature, 'cognitive'—those most commonly measured in the psychology/learning literature, and 'social'—those most commonly measured in the social insect literature. We do not presume this list to be exhaustive, but instead wish to provide examples for researchers interested in studying behavioural syndromes in social insects.

Table 3. Mechanisms that affect behavioural variation presented in the behavioural syndrome and social insect literature

	Behavioral syndrome literature	Social insect literature

Genetic mechanisms	Aggression
	  Kralj-Fiser *et al.* (2010)
	Boldness/shyness
	  Fairbanks *et al.* (1999), Jones *et al.* (2011) and
	    Kinnally *et al.* (2006)
		Learning
		  Chandra *et al.* (2000)
		Division of labour (general)
		  Herb *et al.* (2012), Fewell & Page (1993), Page
		    et al. (1992), Robinson & Page (1989),
		    Robinson *et al.* (1994), Smith *et al.* (2008) and
		    Stuart & Page (1991)
		Hygienic behaviour
		  Robinson & Page (1988)
		Foraging
		  Ben-Shahar *et al.* (2002), Fewell & Page (1993),
		    Hunt *et al.* (2007), Ingram *et al.* (2005), Page
		    et al. (1998, 2012*b*), Pankiw *et al.* (2002),
		    Robinson & Page (1989), Scheiner *et al.* (2001)
		    and Waddington *et al.* (1998)
		Defence
		  Breed *et al.* (2004), Hunt *et al.* (2007), Moore
		    et al. (1987) and Robinson & Page (1988)
		Reproductive
		  Cahan & Keller (2003), Graff *et al.* (2007), Page
		    et al. (2012*b*), Schwander *et al.* (2007, 2010),
		    Smith *et al.* (2008), Volny & Gordon (2002)
		    and Weiner & Toth (2012)

Physiological mechanisms	Aggression
	  Brown *et al.* (2003), Bryant & Newton (1994),
	    Cutts *et al.* (1998) and Koolhaas *et al.* (2007)
	Exploratory (activity)
	  Careau *et al.* (2008) and Chappell *et al.* (2004)
	Boldness/shyness
	  Huntingford *et al.* (2010)
	Proactive/reactive
	  Careau *et al.* (2008) and Koolhaas *et al.* (2007)
	Foraging
	  Mathot *et al.* (2009)
		Aggressive
		  Tibbetts & Huang (2010)
		Cooperative
		  Lin *et al.* (1999)
		Division of labour (general)
		  Blanchard *et al.* (2000), Dolezal *et al.* (2012),
		    Robinson (2009), Robinson & Huang (1998)
		    and Toth *et al.* (2009)
		Hygienic behaviour
		  Spivak *et al.* (2003)
		Foraging
		  Dolezal *et al.* (2012), Fewell & Page (1993),
		    Giray *et al.* (2005), Robinson & Page (1989)
		    and Seid & Traniello (2006)
		Reproductive
		  Brent *et al.* (2006), Giray *et al.* (2005), Page *et al.*
		    (2012*b*) and Smith *et al.* (2008)

Experiential mechanisms	Aggression
	  Del Giudice *et al.* (2011) and Niemelä *et al.*
	    (2012)
	Exploration (activity)
	  Del Giudice *et al.* (2011), Heifetz & Applebaum
	    (1995) and Lihoreau *et al.* (2009)
	Boldness/shyness
	  Del Giudice *et al.* (2011) and Niemelä *et al.*
	    (2012)
	Foraging
	  Lihoreau *et al.* (2009)
		Exploratory (activity)
		  Seeley *et al.* (1998)
		Cooperative
		  Lin *et al.* (1999)
		Division of labour (general)
		  Greene & Gordon (2003, 2007), Powell &
		    Tschinkel (1999), Robinson & Huang (1998)
		    and Wilson (1985)
		Foraging
		  Anderson & Ratnieks (1999), Fewell & Page
		    (1993), Pankiw *et al.* (2002) and Robinson &
		    Page (1989)
		Reproductive
		  Kamakura (2011) and Suryanarayanan *et al.*
		    (2011*a*)

Mechanisms are not mutually exclusive. Note that each literature has focused on defining mechanisms for very different sets of behavioural axes: behavioural syndrome research has focused on mechanisms for the classically studied behavioural types whereas social insect literature has focused on mechanisms for primarily social behavioural types.

(*foraging*) gene in honey bees and harvester ants affects whether an individual will be more likely to engage in brood care or foraging tasks, irrespective of age (Ben-Shahar *et al.*, 2002; Ingram, Oefner & Gordon, 2005). Differences in gene expression might be the result of experience, nutrition, age, or genotype; and often expression patterns are conserved across species (e.g. expression of *hexamerin* storage proteins often correlates with reproductive caste differentiation: Smith *et al.*, 2008). Epigenetics, i.e. the effects of DNA methylation, is a relatively new area of research, and its role on behavioural type is beginning to be investigated in social insects, both in terms of reproductive (Weiner & Toth, 2012) and non-reproductive (Herb *et al.*, 2012) division of labour.

(*ii*) *Physiology.*   Social insect workers often change their role or specialisation over the course of their life, referred to as temporal polyethism (Table 1; Seeley, 1982). In the behavioural syndrome literature, switching between behavioural types is referred to as episodic personality (Table 1; Pronk, Wilson & Harcourt, 2010). In honey bees, transitions tend to occur in a particular order (Seeley, 1982), but this is not necessarily the case for all social insects. In some species, task repertoire (the number of tasks an individual performs) expands with age (Seid & Traniello, 2006), whereas in others, the order of task-switching is seemingly random (Gordon *et al.*, 2005; Jandt, Huang & Dornhaus, 2009).

Often, juvenile hormone (JH) influences the task an individual performs (Table 3; Robinson, 1987; Hartfelder, 2000; Giray, Giovanetti & West-Eberhard, 2005; Brent *et al.*, 2006; Dolezal *et al.*, 2012) (but see Cameron & Robinson, 1990), and in some cases, change in corpulence (fat content) also correlates with the performance of certain tasks (Table 3; Toth & Robinson, 2005; Robinson, 2009; Robinson *et al.*, 2009; Daugherty, Toth & Robinson, 2011), but this is not necessarily true for all social insects (Couvillon *et al.*, 2011). Research on *Polistes dominulus* wasps has shown that JH concentration changes during aggressive encounters (Tibbetts & Huang, 2010), and so it might be directly related to an individual's aggressive behavioural type.

It is indeed possible that temporal polyethism, caused by physiological change over an individual's lifetime, might also be a type of 'maturation' or 'ageing' syndrome — that is, several associated traits are ultimately caused by ageing, and the ageing process could differ among individuals (Dingemanse *et al.*, 2010). Therefore, it is important to consider maturation, as well as unavoidable senescence, as plausible hypotheses both to explain the evolution of temporal polyethism and of behavioural syndromes in general.

(*iii*) *Environment.*   There are a variety of environmental factors that can influence behavioural type (Table 3): abiotic factors (e.g. temperature), ecological environment (e.g. food availability and/or competition), and social environment (e.g. interaction rates and communication signals). Early developmental influences are often particularly important. For example, early developmental influences, such as larval feeding or maternal effects can lead to size, reproductive, and in some cases distinct caste differences (Wheeler, 1986; Winston, 1987; Couvillon & Dornhaus,

2009; Kamakura, 2011; Suryanarayanan *et al.*, 2011*a*; Suryanarayanan, Hermanson & Jeanne, 2011*b*). Thus, certain individuals that take care of brood could determine the behavioural types within a colony either through direct communication (Suryanarayanan & Jeanne, 2008) or by manipulating the way in which larvae are raised (Pereboom, Velthuis & Duchateau, 2003; Couvillon & Dornhaus, 2009). Such manipulations during development will likely have a strong influence on the behavioural type of an individual which might then carry over across contexts or over time (Bergmüller, Schürch & Hamilton, 2010).

In addition to events that happen during development, the interactions of adult workers (or lack thereof) in a colony might also determine the behaviour of individuals. Studies in which individuals performing a certain task are removed from a colony show that other individuals change which tasks they perform (Gordon, 1989, 1996; Pinter-Wollman *et al.*, 2012*b*, and references therein). Thus, the social environment is an important factor in determining how individuals behave.

(*d*) *Fitness consequences of intra-colony behavioural variation*

Because individuals might not be infinitely flexible, and because switching between behavioural types (see Table 2 for examples) can be costly or inefficient, colonies can circumvent these constraints by maintaining mixtures of individuals with different behavioural types. For example, if the distribution of flowering plants changes within a season or even within a day (O'Neal & Waller, 1984), maintaining a mixture of foragers that vary along the speed-accuracy behavioural axis could allow colonies to respond more quickly to environmental fluctuation (Burns & Dyer, 2008). That is, slower, more accurate individuals can bring large quantities of food back to the colony when food abundance is constant, whereas faster, 'sloppier' individuals might be more efficient at exploiting resources in more frequently changing environments (Raine & Chittka, 2008, 2012; Chittka, Skorupski & Raine, 2009). A colony containing a mixture of these types might thus be able to handle different environments despite individual inflexibility or carryover.

In the ant *Temnothorax longispinosus* and the social spider *Anelosimus studiosus*, groups with a mixture of aggression types tend to have higher fitness than groups with only one type (Modlmeier & Foitzik, 2011; Pruitt & Riechert, 2011). In ant colonies, aggressive individuals defend the nest whereas docile individuals take care of brood. In the spiders, more aggressive individuals are faster to attack and subdue prey (leading to an increase in foraging performance), whereas less aggressive (more docile) individuals promote group cohesiveness by not escalating aggression during foraging and/or contest encounters (the absence of docile individuals can lead to excessive within-group fighting, cannibalism of colony mates, and group disbandment).

However, maintaining a mixture of relatively inflexible behavioural types could also incur costs to the colony. For example, aggressive *Rhytidoponera confusa* ants are not only more aggressive towards other ants, they are also more likely to lunge at or bite their own nestmates (Crosland, 1990).

This suggests a clear trade-off in aggressive behavioural differences, as well as a limited flexibility in the ability to 'shut-off' the aggressive phenotype across contexts.

Not all behaviours are inflexible, however. Pearce, Huang & Breed (2001) showed that although nurse and guard bees differ in their level of aggressiveness in the summer, these task groups could not be distinguished in the winter months, suggesting that aggressive behaviour can be somewhat plastic.

Numerous studies have found benefits to maintaining variation within colonies (Porter & Tschinkel, 1985; Cnaani & Hefetz, 1994; Page *et al.*, 1995*a*; Weidenmüller, 2004; Powell & Franks, 2005; Billick & Carter, 2007; Mattila & Seeley, 2007; Dornhaus, 2008; Powell, 2008; Modlmeier, Liebmann & Foitzik, 2012; J. M. Jandt & A. Dornhaus, in preparation), but it is not always clear why exactly variation (as opposed to all individuals being of one optimal type) is beneficial. There is a need to develop theory that helps us to understand under which circumstances we would expect variation to be a better solution than one stable optimal type—not only with regards to division of labour, but also in terms of variation in other behavioural types such as aggression or exploratory behaviour.

(2) Variation among colonies

The reproductive unit of social insects on which natural selection acts is the colony. Therefore, consistent differences among colonies could have important implications on the success of certain phenotypes over others, influencing population structure. Variation among colonies in a certain behaviour might in itself have important ecological consequences. For example, colonies of more aggressive species could out-compete other colonies through interference competition (Davidson, 1998; Rowles & O'Dowd, 2007). If colony behaviour is also consistent across contexts, we might find interesting relationships between the success of a colony in one situation and its success or failure in another. For example, if there is a relationship between aggression and exploration, colonies that are both exploratory and aggressive might be better at invading new habitat. However, when these two behaviours are not correlated, exploratory colonies may find new habitat, but be quickly displaced by aggressive colonies (Cote *et al.*, 2010; Fogarty, Cote & Sih, 2011; Sih *et al.*, 2012).

Aside from work to investigate the heritability of pollen-foraging behaviour (Page *et al.*, 1995*a*,*b*; Page, Fondrk & Rueppell, 2012*a*), colony-level behavioural syndromes have received comparatively little attention. However, the behavioural repertoires of colonies include traits measured in classical behavioural syndromes (e.g. aggressiveness), cognitive behavioural syndromes (e.g. learning ability), and social behavioural syndromes (e.g. communication: see Table 2). For example, Crosland (1990) showed that colonies of the ant *Rhytidoponera confusa* consistently exhibited high or low levels of aggression towards non-nestmates. This classical behavioural type of aggression has also been shown to vary among colonies of the invasive Argentine ants (Suarez *et al.*, 2002; Buczkowski & Silverman, 2006), a colony trait that

might help to explain the highly invasive success of certain colonies. Colonies also vary in cognitive behavioural types. For example, bumble bee colonies vary in their learning speed and foraging success (Raine *et al.*, 2006*b*; Raine & Chittka, 2008, 2012; Ings, Raine & Chittka, 2009; Gill, Ramos-Rodriguez & Raine, 2012). Colonies also differ in the degree to which they perform tasks such as foraging, defence, brood care, or hygienic behaviour. For example, colonies of harvester ants and honey bees vary in foraging activity levels (Gordon, 1991; Cole *et al.*, 2010; Gordon *et al.*, 2011; Wray, Mattila & Seeley, 2011) and in how they regulate foraging activity (Gordon *et al.*, 2011). Colonies of honey bees and black harvester ants (*Messor andrei*) also differ in defensive response (Wray *et al.*, 2011; Pinter-Wollman, Gordon & Holmes, 2012*a*). Furthermore, Africanized honey bees differ from European honey bees in defensive response (Collins *et al.*, 1982), as well as a number of other traits related to the pollen-hoarding syndrome (Pankiw, 2003).

Like workers, colonies also exhibit consistent behavioural variation across situations. For example, in both honey bees and black harvester ants, colonies vary consistently in their response to food and to disturbance, which are correlated with one another, producing a behavioural syndrome (Wray *et al.*, 2011; Pinter-Wollman *et al.*, 2012*a*). That is, colonies that send out many workers to forage also send out many workers to defend the nest when disturbed. These behavioural syndromes might have important fitness consequences (Wray *et al.*, 2011) and could result from constraints on colony behaviour. For example, workers might follow similar local rules in various situations (e.g. patrolling and foraging; Gordon *et al.*, 2011), and external features such as nest structure could influence how a colony behaves in various situations (Pinter-Wollman, 2012; Pinter-Wollman *et al.*, 2012*a*).

(a) Mechanisms underlying variation among colonies in behavioural type

(*i*) *Colony genetics.* The genetic make-up of a social insect colony is generally represented by the genotype of the queen and the number of unrelated males she mates with. The extent to which workers vary genetically might have an effect on the behavioural type observed at the colony level (see Section II.1*c*). Colonies with greater genetic variation might achieve better rates of thermoregulatory homeostasis (Jones *et al.*, 2004; Oldroyd & Fewell, 2007), foraging ability (Page *et al.*, 1995*a*; Mattila, Burke & Seeley, 2008), or productivity and fitness (Mattila & Seeley, 2007). Whether the behavioural type or genotype of a queen can be used to predict colony behavioural type has yet to be studied (but see Section II.2*a.iii*), although there is evidence that honey bee male genotype can be used to predict behavioural type in an offspring colony (Page *et al.*, 2012*a*).

(*ii*) *Colony composition and emergent behaviour.* The frequency of individual behavioural types in a colony might affect colony behavioural type and/or colony performance (Hillesheim, Koeniger & Moritz, 1989; Tsuji, 1994 Paleolog, 2009; Michelena *et al.*, 2010; J. M. Jandt & A. Dornhaus,

in preparation). Consistent individual differences among colonies might emerge both from variation in the average behavioural types of their workers and from the distribution of worker behavioural types (Pinter-Wollman, 2012). For example, if ant colonies vary in aggressive behaviour, this could be caused by the number of highly aggressive ants present in each colony (Crosland, 1990). That is, there might be many individuals of an aggressive caste (e.g. high numbers of soldiers in an aggressive colony), or alternatively there could be a high frequency of aggressive individuals within each caste.

Because the collective behaviour of colonies is an emergent property of individual workers that follow simple, local rules (Camazine *et al.*, 2001; O'Donnell & Bulova, 2007*a*; Sumpter, 2010), careful consideration is needed when measuring colony behaviour. For example, to determine colony aggression, it is not enough to sample a few workers, put each in an aggression assay against one other worker and sum their response to generate a colony aggression level. A more appropriate test would be to place two colonies in a situation where they are competing over a scarce resource (such as food or a nest site). Using entire colonies allows us to observe colony-level behaviours without the confounding factor of subsampling heterogeneous colony populations. That is, the sum of the individual behaviours might not necessarily represent the behaviour of the whole colony.

The relationship between colony composition and emergent colony behaviour might be non-linear, i.e. just a few individuals could significantly change the behaviour of a group or population as a whole (Sih & Watters, 2005; Sih, Hanser & McHugh, 2009). The queen of a social insect colony, as the primary reproductive, might be considered a conspicuous type of keystone (or key) individual (Table 1), but rarely does she take an active role in influencing the behaviour of other workers in the colony in non-reproductive contexts (Jeanson, 2012). Workers might also take on key roles in the colony, either as highly active or aggressive individuals that affect the overall performance of a colony (Paleolog, 2009), or as informed individuals that influence nest-site selection decision-making (Couzin *et al.*, 2005). For example, in honey bees, the presence of only a few aggressive individuals drastically changes the behaviour of the colony, because the individuals performing the task are a non-random (more aggressive) subset of the colony (Paleolog, 2009). So, although there are only a few aggressive individuals, those are the ones performing the task resulting in an aggressive colony (Paleolog, 2009). In *Anelosimus studiosus* spiders, the presence of only a few aggressive individuals drastically changes the efficiency with which colonies feed, and alters the nature of a number of species interactions (Pruitt & Ferrari, 2011). In these examples a few aggressive individuals can create a bias towards the colony becoming highly aggressive.

Key individuals (also referred to as catalysts, performers, and organisers; Robson & Traniello, 1999) can assume various roles. As colony behavioural outcomes might be described in a number of ways (foraging success, fecundity, activity, etc.), who is recognized as a keystone individual might differ based on which output is being measured. Individuals performing keystone roles could increase performance by better facilitating information flow through the colony (Couzin *et al.*, 2005; Pinter-Wollman *et al.*, 2011), facilitate an increase in the rate of activity in other workers (Cao *et al.*, 2009), motivate nestmates to begin foraging (O'Donnell, 2006; Molet *et al.*, 2008), communicate more avidly with others in the colony (Cao *et al.*, 2007), or increase cohesion within the colony. For example, in honey bee colonies, certain individuals (i.e. 'activators') are more likely to roam the nest and activate idle nestmates by using vibration signals (Cao *et al.*, 2009). An interesting next step will be to determine whether the number or proportion of activators in the nest can predict overall activity level of the colony. In yet another type of keystone role, elite workers (or 'generalist elites') perform many tasks (unlike task specialists that tend to focus on only one task; Table 1), with little or no help from other workers (Dornhaus, 2008; Pinter-Wollman *et al.*, 2012*b*). For example, in *Leptothorax allardycei*, over 50% of the colony has been described as inactive—leaving the majority of tasks to be performed by the remaining workers (Cole, 1986). If this percentage were to vary, the behavioural type of the colony might change in the degree to which tasks are performed. Understanding keystone roles, the types of individuals that engage in those roles, and the rate of turnover within colonies is an important issue in any social group (including humans), and detailed studies can readily be conducted using social insects, e.g. *via* removal of diligent workers (Pinter-Wollman *et al.*, 2012*b*, and references therein).

(*iii*) *Colony environment.*   Once a colony is established, the role of the queen rarely extends beyond functioning as a reproductive organ. Therefore, in addition to the difficulty of studying queen behaviour in the nest, research on queens is limited to what they do while founding a colony (Fewell & Page, 1999; Cahan & Fewell, 2004). Foundresses (pre-egg-laying reproductive females) vary in their method of dispersal (founding, swarming, budding, joining) (Augustin, Santos & Elliot, 2011). For example, a *Temnothorax longispinosus* ant foundress can either fly off and found her own colony (independent foundress) or join an already established nest (dependent foundress) (Howard, 2006). The level of conspecific tolerance seen during the initial nesting phase can also vary. For example, *Polistes dominulus* paper wasp foundresses can independently initiate or co-found colonies, and the number of foundresses can vary across colonies (Zanette & Field, 2011).

What remains unclear is how variation in queen behaviour translates into variation in colony behaviour. If queens vary inherently in traits that affect their habitat selection, this could have long-term effects on the colony, e.g. bold queens might found colonies in a densely populated, but high-quality, location and shy queens might establish further from other colonies but perhaps in locations with scarcer resources. This variation in microhabitat could influence how early resources for initial brood-rearing are acquired, in turn, impacting colony behavioural type. Once established, the on-going role of the queen in the colony can vary. In

eusocial naked mole rats, *Heterocephalus glaber*, for example, queens have been shown to activate lazy workers (Reeve, 1992). If queens vary in their thresholds to tolerate inactive workers, this might impact the overall activity of the colony.

(b) *Fitness consequences of colony behavioural syndromes*

A colony's behavioural type (e.g. in terms of aggressiveness, defensive response, foraging activity, or undertaking) can influence its fitness (in terms of colony productivity or winter survival; Wray *et al.*, 2011). As a behavioural syndrome inherently suggests limited behavioural plasticity, behavioural syndromes are often associated with some kind of trade-off. Beneficial responses to one stimulus might be coupled with sub-optimal behaviour in response to others. These costs might not be apparent until a colony is put in an alternative context. For example, more aggressive or exploratory colonies might out-compete other colonies in areas of limited resources. However in areas with plentiful resources, excessive or unnecessary contests with other colonies could result in losses of brood or workers, with no additional resources gained.

The fitness consequences of behavioural syndromes at the colony level are difficult to study because of the long generation time of social insect colonies and the paucity of studies on their reproductive success. However, indirect measures of colony success such as growth and foraging activity might provide some insights about the importance of behavioural syndromes at the colony level. For example, *Pogonomyrmex barbatus* ant colonies vary in how they regulate their foraging behaviour, which affects how much they forage on a given day (Gordon, 1991; Gordon *et al.*, 2011) and potentially how much food the colony can store. Honey bee colonies bred for better hygienic behaviour (efficient removal of dead larvae) are less susceptible to disease (Lapidge, Oldroyd & Spivak, 2002), possibly increasing overall health. Other research is beginning to show that connections between colony traits or behavioural types might have significant impact on colony performance and fitness (Suarez *et al.*, 2002; Buczkowski & Silverman, 2006; Raine & Chittka, 2008; Paleolog, 2009; Gordon *et al.*, 2011; Wray *et al.*, 2011; Modlmeier *et al.*, 2012; Pinter-Wollman *et al.*, 2012*a*).

III. INSIGHTS FROM BEHAVIOURAL SYNDROMES FOR THE STUDY OF SOCIAL INSECTS

(1) Trade-offs

A common theme in the behavioural syndrome literature is measuring the benefits or costs of an inflexible behavioural type across contexts. For instance, consistently bold and aggressive individuals often enjoy increased foraging success (Sih *et al.*, 2003; Short & Petren, 2008), growth rates (Biro & Stamps, 2008), and superior performance during contests (Pruitt & Riechert, 2009), but also suffer increased susceptibility to predation or parasites (Fig. 1A; Pontier *et al.*,

1998; Biro *et al.*, 2006). Other trade-offs can be less intuitive, particularly those involving social interactions. For example, male western blue birds (*Sialia mexicana*) exhibit a syndrome of aggressiveness between nest defence and male-male competition that ultimately results in decreased fitness. Highly aggressive males engage in excessive male–male contests during the breeding season, and consequently fail to provision nesting females with necessary food. This results in disrupted incubation patterns, as females must leave the nest to forage, reducing offspring survival (Duckworth, 2006).

Although recent literature has challenged the potential of behavioural syndromes to set evolutionary constraints (Bell, 2005; Dingemanse *et al.*, 2007), a sizeable (and growing) body of literature continues to document numerous trade-offs associated with behavioural consistency. It is yet unclear whether these trade-offs are the result of proximate constraints such as genetic linkage. Optimality theory suggests selection should act against limited behavioural plasticity; however there might be adaptive benefits (Sih *et al.*, 2004*a*). For example, limited plasticity prevents animals from making more costly errors in an unpredictable environment (Sih, 1992). Conversely, the social insect literature shows examples of trade-offs being the result of genetic linkage. For example, the reproductive ground-plan hypothesis proposes that different levels of pollen-hoarding in honey bee foragers is the result of evolutionary co-option of the female reproductive system (Amdam & Page, 2010), and genetic linkage between foraging behaviour, reproduction (Graham *et al.*, 2011) and at least two genes (*HR46* and *PDK1*) has been demonstrated (Wang *et al.*, 2009).

Because consistent traits across different contexts can produce performance trade-offs, determining the source and magnitude of these trade-offs is a continuing goal of behavioural syndromes research. Furthermore, until recently, colony-level behavioural variation has not received as much attention as within-colony variation (see Table 2). It could be useful to examine under what conditions within-population variation can evolve if trade-offs are present, and how those conditions match those where variation persists in populations of non-social animals.

(2) Feedback

Recent work has addressed how behavioural syndromes are maintained in a population. Several authors have suggested that a key mechanism for maintaining consistent differences in behavioural types is the feedback between the individual's behaviour and its state (Luttbeg & Sih, 2010; Wolf & Weissing, 2010), such as the feedback linking an individual's behavioural type and its energy reserves, condition, or social rank. For example, colonies that are quick to exploit a new resource could gain an early benefit, but they might also be easily displaced by a more dominant or aggressive colony and must then locate a new resource pool. These differences in strategy might be the result of differing behavioural types, and are consistently reinforced by the social rank of a colony. A central premise of this frequency-dependent selection has been that the mix of behavioural types in social

groups influences social dynamics and the fitness of each behavioural type. Because social dynamics are important in social insects, understanding how variation in behavioural types in the colony influences individual and group outcomes is an exciting area for future study (Pinter-Wollman, 2012).

(3) Statistical methods

Studies in social insects have illustrated variation in classical, cognitive, and social behavioural types both within and among colonies (Table 2). Quantifying various behavioural types, as well as understanding how variation across multiple behavioural axes might affect colony fitness are topics that are beginning to receive attention in the social insect literature (e.g. see Modlmeier *et al.*, 2012). Scientists studying social insects can draw on advances in statistical methods from the general behavioral syndrome literature for identifying, quantifying, and correlating behavioural types and syndromes across time and context (Sih *et al.*, 2004*a*; Réale *et al.*, 2007; Garamszegi & Herczeg, 2012). Recently, statistical approaches have been reviewed to quantify animal personalities, behavioural syndromes, and behavioural plasticity (Dingemanse *et al.*, 2010; Dingemanse, Dochtermann & Nakagawa, 2012; Garamszegi & Herczeg, 2012). We briefly highlight some points here, but refer the reader to these reviews for detailed analyses of how and when to use various statistical approaches.

Two key analytical tools for behavioural syndrome research are principal component analyses (PCAs) and pairwise correlations. When used together these analyses provide a convenient way to tackle large data sets where some combination of variables could predict behavioural correlations. Factor analyses, structured equation modeling, generalized linear mixed models, and other statistics have also been applied to behavioural syndromes research (Bell & Stamps, 2004; Dingemanse *et al.*, 2010; Garamszegi & Herczeg, 2012), and these approaches can add to the tool kit available to social insect biologists. While these statistical approaches require very large datasets, they help address the point that variation in behavioural flexibility could be as vital as differences in mean trait values. Moreover, when paired with familiar theory on the trade-offs associated with phenotypic plasticity, these approaches provide us with clear and testable predictions on when trait flexibility *versus* consistency should be favoured.

IV. INSIGHTS FROM SOCIAL INSECTS FOR BEHAVIOURAL SYNDROMES

(1) Group-living might affect behavioural type

Although many studies of behavioural syndromes have been conducted on social animals, and many of the commonly studied behavioural axes are inherently social behaviours (see Table 2), the social ecology of behavioural types has not yet received much experimental attention. For example,

how does a mix of behavioural types in a group influence individual behaviours [social plasticity (Kurvers *et al.*, 2010) or group outcomes (Crosland, 1990; Sih & Watters, 2005; Eldakar *et al.*, 2009; Paleolog, 2009; Pruitt & Riechert, 2011; Schürch, Rothenberger & Heg, 2011)]? Work on social insects has shown that indirect genetic effects (whether offspring are raised by the parent or siblings) can influence colony phenotype (Linksvayer, 2006). Colonial living can also result in greater variation in individual experiences, which can further alter individual behavioural tendencies (Bergmüller *et al.*, 2010; Pruitt *et al.*, 2012). Studies of social insect colonies have a long history of looking at how individuals and their behaviours collectively produce group outcomes (Oster & Wilson, 1978), and there are a variety of examples where feedback between the individual and the rest of the group might affect colony behaviour (Fig. 1B; Crosland, 1990; Beverly *et al.*, 2009; Paleolog, 2009).

Variation in behavioural type within a group could reduce competitive interactions among group members (reviewed in Ratnieks & Reeve, 1992; Bergmüller *et al.*, 2010). Furthermore, the spatial organisation of individuals in a colony might be analogous to niche partitioning measured in behavioural ecology (Sendova-Franks & Franks, 1995; Beverly *et al.*, 2009; Jandt & Dornhaus, 2011; Dall *et al.*, 2012). Recently, social network theory has been employed to study the development and maintenance of behavioural types within a social group (Krause, Lusseau & James, 2009; Sih *et al.*, 2009). There are a variety of examples of the use of network theory to understand how interactions affect group behaviour in social insects as well (Blonder & Dornhaus, 2011; Pinter-Wollman *et al.*, 2011). We propose that a link between models developed on social networks and on behavioural syndromes could benefit both the study of social insects and animal behaviour in general.

The study of behavioural syndromes can also benefit from exploring models that show how division of labour emerges from feedback mechanisms and interactions among workers, and models that predict how the interactions of those workers produce complex patterns and colony behaviour (Fig. 1B; Camazine, 1991; Theraulaz & Bonabeau, 1995; Bonabeau, Theraulaz & Deneubourg, 1998; Theraulaz, Bonabeau & Deneubourg, 1998; Camazine *et al.*, 2001; O'Donnell & Bulova, 2007*b*). Social feedbacks can facilitate the maintenance of multiple behavioural types within the nest (Gordon, 1989, 1996; Reeve & Nonacs, 1997; Bergmüller *et al.*, 2010). For example, small differences in response thresholds can lead to stable long-term differences in behaviour, even among non-social animals (Fewell & Page, 1999), and the social environment might prevent or promote transitions among tasks (Gordon, 1989; Amdam *et al.*, 2005; Gordon *et al.*, 2005). Researchers of behavioural syndromes are beginning to explore how positive feedback loops might maintain consistent behavioural types (Luttbeg & Sih, 2010). These models can guide further study of how complementary behavioural types in non-social insects can affect group dynamics, and how these in turn can determine the behaviour and fitness of individuals.

(2) Mechanisms affecting behavioural type

A crucial question in behavioural syndrome research is: what are the mechanisms that affect behaviour? Genetic, hormonal, and experiential mechanisms that could interact and predispose an individual to exhibit a particular social behavioural type have been well studied in social insects (see Section II.1*c* and Table 3). Changes in hormone levels (Robinson, 1987; Giray *et al.*, 2005; Dolezal *et al.*, 2012) and gene expression (Hunt *et al.*, 2010), often associated with a change in social environment (Amdam *et al.*, 2005) affect caste determination and division of labor (Robinson, 1987; Wheeler, Buck & Evans, 2006; Toth *et al.*, 2009; Amdam & Page, 2010; Hunt *et al.*, 2010), cooperative behaviour, in terms of worker egg production (Lin *et al.*, 1999), and aggressive behaviour (Pearce *et al.*, 2001; Tibbetts & Huang, 2010). For example, genetic linkage between foraging and reproductive behaviour (Wang *et al.*, 2009) might not only limit an individual's behavioural plasticity (or act as a 'constraint'), but could also have been an adaptive precursor that allowed solitary ancestors to evolve into social groups (Amdam *et al.*, 2004; Hunt & Amdam, 2005; Smith *et al.*, 2008; Toth *et al.*, 2009; Hunt *et al.*, 2010; Page *et al.*, 2012*b*).

Morphological differences have also been implicated as a mechanism underlying behavioural syndromes (Sih *et al.*, 2004*b*). However, it is often difficult to modify the morphology of an organism to determine which aspects of an individual's morphology have the greatest effects on behaviour. Insect colonies provide a unique system in which the demography and composition of a colony can be manipulated, i.e. whole task groups or castes can be removed or proportions adjusted (Porter & Tschinkel, 1985; Cnaani & Hefetz, 1994; Roux & Korb, 2004; Billick & Carter, 2007; J. M. Jandt & A. Dornhaus, in preparation). The nest structure can be considered an extended phenotype of the colony (Tschinkel, 2004), and changes to this structure, i.e. to nest morphology, could have an effect on colony-level behaviours (Pinter-Wollman *et al.*, 2012*a*). Both colony composition and nest architecture can be manipulated to determine the relative role each plays in the maintenance of a behavioural type.

(3) Development of behavioural types across levels of organisation

When examining the behavioural type of an individual, its behaviour is often examined at different stages or in response to different stimuli (Bell & Stamps, 2004; Briffa, Rundle & Fryer, 2008; Bell, Hankison & Laskowski, 2009; Biro, Beckmann & Stamps, 2010; Dingemanse *et al.*, 2010). It would be considerably more difficult to monitor the changes of individual cells in a vertebrate brain or body to understand how the parts affect the behavioural type of the individual, but we concede that these often play a significant role. However, using social insects we can monitor how variation in worker development [e.g. change in physiology and/or gene expression patterns (Kocher *et al.*, 2010; Herb *et al.*, 2012)], change in colony composition (i.e. the development of the superorganism), and feedback between levels of organisation (Kocher

et al., 2010) can affect behavioral type (Fig. 1B). The insight that can be gained from understanding the biological interactions within a social group and how that translates to colony-level behaviours can provide important insights to those who study behavioural syndromes in solitary organisms.

V. FUTURE DIRECTIONS

In the field of social insects, it has long been acknowledged that variation among workers might affect colony fitness by providing a mechanism for division of labour. Here we have reviewed examples of variation along multiple behavioural axes both at the colony and individual levels. While division of labour has long been speculated as critically important in enhancing colony fitness (Oster & Wilson, 1978), the behavioural syndromes approach provides an alternative method for determining the extent to which variation in behavioural types within colonies (including, but not limited to, those associated with caste and division of labour) and among colonies might affect fitness and ecology. While we acknowledge there are a variety of ways in which the behavioural-syndrome approach can be used to create insightful and important questions, we propose in particular the following three areas that would benefit from the attention of eager social-insect/behavioural syndrome enthusiasts.

(1) What are the adaptive reasons for colonies, or groups of individuals, to maintain mixtures of behavioural types?

As mentioned above (Sections II.1*d*, and II.2*a*), many studies have found benefits to maintaining variation within colonies (Porter & Tschinkel, 1985; Cnaani & Hefetz, 1994; Page *et al.*, 1995*a*; Weidenmüller, 2004; Powell & Franks, 2005; Billick & Carter, 2007; Mattila & Seeley, 2007; Dornhaus, 2008; Powell, 2008; Modlmeier *et al.*, 2012; J. M. Jandt & A. Dornhaus, in preparation). However, it is not always clear why exactly variation (as opposed to all individuals being of one optimal type) is beneficial. Furthermore, these studies can be expanded to include non-social-insect group-dwelling species (Sih & Watters, 2005; Eldakar *et al.*, 2009; Pruitt & Riechert, 2011).

Trait complexes could be the product of genetic or physiological linkage, rather than adaptive combinations for optimal division of labour. It is possible that mixtures of behavioural types within a colony (e.g. aggressive or exploratory types) shaped the way in which task groups (e.g. guards or patrollers) have evolved. We find correlations among multiple physiological factors that affect the behaviour of individual workers—both within and between castes—that are not obviously explained by the requirements of the tasks themselves.

Mixtures of behavioural types within a colony might affect the flexibility of the colony to react to changing environmental conditions. For example, colonies could become more active when environmental conditions are

favourable (Gordon, 1991; Cole *et al.*, 2010; Pinter-Wollman, 2012). The more variation among workers, the more types of individuals are available for each ecological condition, and indeed, high variation among workers increases colony productivity (Page *et al.*, 1995*a*; Jones *et al.*, 2004; Mattila & Seeley, 2007; Oldroyd & Fewell, 2007; Mattila *et al.*, 2008; Modlmeier & Foitzik, 2011). Differences in colony ability to respond to changing conditions could be critical in the modern world of human-induced rapid environmental change (HIREC; Sih, Ferrari & Harris, 2011), including changes in climate and habitat, and exposure to novel species or contaminants.

Finally, behavioural variation might persist in a group *via* social heterosis (Nonacs & Kapheim, 2007, 2008). Social heterosis is a mutually beneficial process that occurs when individuals benefit by associating with genetically dissimilar individuals. Under such circumstances, groups (or demes) of mixed genotype outperform monotypic groups and singleton individuals of any genotype. Potential mechanisms behind social heterosis include reduced competition among group constituents, complimentary skill pools, or instances where individuals are incapable of approximating the optimal genotype for a population. Importantly, social heterosis is sufficient in itself to maintain genetic diversity at one or more loci in the face of genetic drift (Nonacs & Kapheim, 2007, 2008). The predicted outcomes of social heterosis are high genetic diversity (and heritability) of functional traits (Stirling, Réale & Roff, 2002; Nonacs & Kapheim, 2007), and a positive association between within-group trait variation and fitness for group constituents. Both patterns have been observed in numerous test systems, from microbes (Vos & Velicer, 2006), to primates (Wooding *et al.*, 2006). In social insects, social heterosis might be an explanation as to why unrelated individuals will cooperate with one another during nest-founding in some species (Tschinkel, 1998; Queller *et al.*, 2000; Jeanson & Fewell, 2008; Leadbeater *et al.*, 2010; Zanette & Field, 2011).

(2) Do colonies differ in their degree of cooperation?

A growing field in behavioural syndrome research is to identify the degree to which individuals or groups vary in cooperativeness. A cooperative behavioural type could be measured in terms of group cohesion, lack of within-group conflict, short time spent on tasks devoted to self- *versus* group-maintenance, and low effort spent on reproduction (or competing to reproduce). Social insect colonies are generally assumed to be highly cooperative, yet extreme aggression, worker reproduction, and over-policing of queen-laid eggs are a few examples of within-colony non-cooperative (or cheating) behaviour (Bourke, Have & Franks, 1988; Schmid-Hempel, 1990; D'Ettorre, Heinze & Ratnieks, 2004; Wenseleers & Ratnieks, 2006*a*). Along with the examples listed above, we might measure colony-level cooperation based on the proportion of individuals that are inactive, or regularly refrain from working (Lindauer, 1952; Herbers, 1983; Cole, 1986; Dornhaus *et al.*, 2008; Jandt & Dornhaus, 2009). These inactive individuals might be a reserve set of

workers, or they might be selfishly hoarding their fat reserves and avoiding risky tasks to gain an opportunity to reproduce (Lindauer, 1952; Michener, 1964; Jandt & Dornhaus, 2011). While inactive individuals have been identified in many social insect species, it is unclear whether the proportion of 'lazy' individuals varies across colonies and how that might affect colony fitness.

An additional method for measuring cooperativeness is to examine worker policing behaviour—that is, some workers will regularly inspect the eggs laid in the nest and will eat those that were not laid by the queen (Ratnieks & Reeve, 1992; Wenseleers & Ratnieks, 2006*b*). Some individuals occasionally 'make a mistake' and eat queen eggs too, although often at a lower rate (D'Ettorre *et al.*, 2004). Degree of cooperation might be measured by examining the variation across colonies in the ratio of policing queen eggs *versus* worker eggs, and how that might affect colony fitness.

If colonies differ in how cooperative they are, what will this mean ecologically? Will more cooperative colonies have an ecological advantage in some environments, whereas less cooperative colonies have an advantage in others? Argentine ant colonies that have successfully invaded urban areas are less aggressive (and, hence, more cooperative) with conspecific colonies than those that remain in their native range (Buczkowski, 2010). That is, colonies interact and cooperate with one another, and ultimately end up forming 'supercolonies', a phenotype that allows them aggressively to expand and dominate the areas they colonize (Holway, 1999; Suarez *et al.*, 1999; Holway & Suarez, 2004; Buczkowski, 2010). In native areas, on the other hand, the same species will coexist with a variety of other ant species, and are less likely to form these supercolonies that can aggressively out-compete other species for territory. The theoretical basis for the evolution, maintenance and consequences of individual variation in cooperation has been developed in the behavioural syndrome literature (Bergmüller *et al.*, 2010).

(3) How does consistency in behavioural type affect task performance when individuals switch task?

The extent to which behavioural type persists over time within an individual, and how this could affect future task performance, has received little attention. In honey bees, for example, genetic factors are linked to how quickly an individual transitions between tasks (Page *et al.*, 1998; Rueppell *et al.*, 2004; Amdam & Page, 2010). Research on the honey bee pollen-hoarding syndrome has shown that this transition time is also linked to learning performance, and a variety of other behavioural types (Page *et al.*, 2012*b*). Incorporating a behavioural-syndromes approach also allows us to ask whether this variation in transition time correlates with classical, cognitive, or social behavioural axes (i.e. do more shy workers take longer to transition between tasks? Do they vary in the time required to master that new task or skill set?). Ultimately, this could reveal why individuals vary

in the time scale over which they become specialised on a given task.

Consistency of behavioural type over time could also affect division of labour. For example, are individuals that exhibit high levels of boldness or aggressiveness as a young nurse more likely to guard when they are older, whereas those that exhibit high levels of exploratory behaviour more likely to forage? What role does senescence, or changes in task based on decreased ability, play in behavioural syndromes? Do individuals change behavioural type as they age? Studies using the behavioural-syndromes approach could be useful when considering how workers maintain task organisation in a decentralized system.

VI. CONCLUSIONS

(1) There are clearly two fields of knowledge, the study of social insects and the study of behavioural syndromes, working in parallel on complementary ideas, yet until recently little effort has been invested in bridging these two fields. For example, researchers interested in studying behavioural syndromes of group-living organisms would benefit from the rich literature in social insects on how social interactions can affect individual decision-making. On the other hand, social insect researchers exploring evolutionary causes and consequences of maintaining behavioural types at multiple levels of social organisation would benefit from theory developed in behavioural syndrome research on trade-offs (Fig. 1A), as well as on statistical methods to analyse these phenomena.

(2) One of the advantages of studying behavioural syndromes in social insects is the ability to compare causes and consequences at multiple levels of social organisation. Because of the tight interplay between behavioural type of individuals and groups, it is clear that to understand behavioural syndromes of social animals it is important to understand the feedback among the levels of social organisation (Fig. 1B).

(3) Monitoring the development of an individual's behavioural type (i.e. changes of individual cells in a vertebrate brain or body to understand how the parts affect the behavioural type of the individual) may be more feasible using social insects. Here, we can monitor how variation in worker development (e.g. change in physiology and/or gene expression patterns), change in colony composition (i.e. the development of the superorganism), and feedback between levels of organisation can affect behavioral type. Furthermore, mechanisms that affect the development of these types, as well as the fitness effects of maintaining syndromes—have been measured both within and between colonies.

(4) We propose that both fields take advantage of the knowledge gleaned from the other to avoid reinventing the wheel too many times.

VII. ACKNOWLEDGEMENTS

VIII. REFERENCES

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