

Personality and social context

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ABSTRACT

There has been considerable interest among biologists in the phenomenon of non-human animal personality in recent years. Consistent variations among individuals in their behavioural responses to ecologically relevant stimuli, often relating to a trade-off between level of risk and reward, have been recorded in a wide variety of species, representing many animal taxa. Research into behavioural variation among individuals has major implications for our understanding of ecological patterns and processes at scales from the level of the individual to the level of the population. Until recently, however, many studies that have considered the broader ecological implications of animal personality have failed to take into account the crucial moderating effect of social context. It is well documented that social processes, such as conformity and facilitation, exert considerable influence on the behaviour of grouping animals and hence that isolated individuals may often behave in a qualitatively as well as quantitatively different manner to those in groups. Recently, a number of studies have begun to address aspects of this gap in our knowledge and have provided vital insights. In this review we examine the state of our knowledge on the relationship between individual personality and sociality. In doing so we consider the influence of the social context on individual personality responses, the interaction between the collective personalities of group members and the expression of those personalities in the individual, and the influence of the personalities of group members on group structure and function. We propose key areas of focus for future studies in order to develop our understanding of this fundamentally important area.

Key words: boldness, bold-shy, behavioural reaction norm, coping style, temperament, group.

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I. INTRODUCTION

(1) Background

In behavioural ecology, personality describes consistently expressed behavioural differences between individuals of the same species that are otherwise similar to one another in terms of age, size and sex (Reale *et al.*, 2007; Sih *et al.*, 2004*a,b*; Sih & Bell, 2008; Wilson, 1998; Wilson *et al.*, 1994). Stable inter-individual differences in behaviour have been seen across numerous contexts, including habitat use, reaction to predation threat, intraspecific aggression and neophobia (Reale *et al.*, 2007). These traits can be arranged into behavioural syndromes, such that behaviour in one context predicts behaviour in another (reviewed by Sih, Bell & Johnson, 2004*a*; Sih *et al.*, 2004*b*; Sih & Bell, 2008), or they can vary independently of one another (e.g. Coleman & Wilson, 1998). The emergence and persistence of individual variation in these and other behaviours may result from adaptive differences in reproductive trade-offs, with risk-prone or risk-averse behaviour being associated with strategies to maximise short- or long-term fitness (Wolf *et al.*, 2007; Smith & Blumstein, 2008).

In recent years there has been a surge of interest in animal personalities (reviewed by Reale *et al.*, 2007; Sih *et al.*, 2004*a,b*; Sih & Bell, 2008; Wilson, 1998; Wilson *et al.*, 1994). Personality has been shown to influence, amongst other things, dispersal (Dingemanse *et al.*, 2003; Cote *et al.*, 2010), reproductive success (Boon, Reale & Boutin, 2007), response to environmental perturbation (Dingemanse *et al.*, 2004), interspecific interactions and competition (Webster, Ward & Hart, 2009) and divergence in habitat use and resource polymorphism (McLaughlin, 2001; Wilson & McLaughlin, 2007).

The period over which many of these studies assess behavioural consistency varies depending upon the design and aims of the study, and the species in question, with researchers selecting time periods that are ecologically relevant to the traits they are studying. Such approaches allow researchers to predict individual behaviour at one time or in one context within that timeframe, based upon earlier responses. It is not always practical or possible to measure behavioural consistency for extended periods of time, nor is this always necessary in order to answer many of the questions posed by researchers interested in the mechanisms, functions and fitness outcomes of individual behavioural variation. In fact, the findings of several studies that have explicitly set out to track the stability of personality traits across ontogenetic development (e.g. Bell & Stamps, 2004; Ray & Hansen, 2005; Schürch & Heg, 2010) suggest that for some species and some behaviours at least, the behavioural responses comprising personality can persist for extended periods of

time and across developmental boundaries and may even endure for the lifetime of the individual.

Behaviour is driven to a large extent by physiology, and it is therefore likely that the behavioural variation that comprises personality differences is underpinned by proximate physiological causes (Koolhaas *et al.*, 2001; Sgoifo *et al.*, 2006; Kralj-Fiser *et al.*, 2007; Kralj-Fiser, Weiss & Kotrschal, 2010, reviewed by Johnsson, Winberg & Sloman, 2006; Koolhaas *et al.*, 2010), which themselves are dependent upon genetic and epigenetic mechanisms (Dingemanse *et al.*, 2002; Drent, van Oers & van Noordwijk, 2003; Wright *et al.*, 2003, reviewed by Groothuis & Carere, 2005; van Oers *et al.*, 2005*a*). Sih & Bell (2008) suggest that within-individual repeatability in behavioural responses over time or across contexts is likely to be controlled by relatively stable proximate mechanisms such as elements of underlying physiology. They argue that less plastic components of the endocrine system should be more important than fluctuating elements in determining the relatively rigid and long-term patterns of behavioural stability described in numerous empirical studies of animal personality. For example, they reason that while hormones can rapidly affect and determine behavioural responses, circulating hormone levels are highly changeable, and may be less important than receptor density in explaining longer term within-individual behavioural consistency. Further, they suggest that behavioural syndromes, which consist of correlations between different behavioural responses (such as aggression and exploration rate, for example) may be accounted for by pleiotropic effects of genes or hormones. Behaviours are linked because they share the same causal basis, and selection favouring intense expression of one behaviour may as a consequence result in intense expression of other behaviours, even when performing such a behaviour appears maladaptive.

The genetic and endocrine systems underpinning behavioural responses are highly complex, and the behaviour expressed by the individual, and its underlying genetic basis, may be separated by many hierarchically arranged steps or stages, which themselves may be subject to feedback and interactions with other systems. This complexity potentially allows for a degree of behavioural flexibility, and the environment, including the social context, that an animal experiences can have considerable influence upon its neuroendocrinology and subsequent behaviour (Kralj-Fiser *et al.*, 2007; Sih & Bell, 2008).

While research has investigated the non-genetic factors which might affect the development of personality traits, for example by inducing or facilitating behavioural phenotypic plasticity, fewer studies have focussed upon understanding the factors which affect the expression of personality traits. In particular, surprisingly few studies have considered the

impact of social context upon individual behaviour, despite the fact that much of the work on personality focussed on species that are facultatively or obligatorily social. Indeed, many, perhaps the majority of studies conducted in this field have examined the behaviour of single, isolated focal individuals, thereby failing to take into account social influences upon the expression of their behaviour. This represents a potentially sizeable gap in our understanding. Sociality has considerable influence on individual behaviour that can serve both to restrict the expression of behavioural responses to the environment, through conformity, and also to promote or enhance them, through facilitation. In a recent paper Dingemanse *et al.* (2010) proposed combining both stable inter-individual variation in levels of responsiveness to a stimulus (personality) and intra-individual responsiveness to changes in the intensity of the stimulus, a measure of individual plasticity, into a single measurement, the behavioural reaction norm. One advantage of the behavioural reaction norm approach is that it accounts for variation in individual responsiveness across environmental gradients, continuous or categorical, while allowing for the possibility that this degree of plasticity might vary between individuals or between different personality types. In the case of social context, this gradient may include the number of group mates present, the local group density, the composition of the group and the nature of the relationships between the focal individual and its group mates. We suggest that the concept of behavioural reaction norms will prove useful in understanding the effects of social context upon the expression of individual personality traits. In this review we argue that we cannot fully understand the ecological and evolutionary significance of personality in social animals without having a firm understanding of the influence of these social processes upon its expression.

(2) Aims and scope

This review has three aims. First, we briefly introduce the social processes which can influence the behaviour of individuals within groups, providing examples for each. Processes such as conformity effects and social facilitation are well documented within the literatures covering social organisation, social learning and anti-predator behaviour, however they have received limited consideration within the field of animal personality.

Second, we review those studies that have examined the influence of sociality upon personality traits. We discuss these studies in relation to three questions:

- (1) Is individual variation for a given personality trait expressed consistently between asocial and social contexts?
- (2) Does group mate identity and the composition of the social group influence the expression of personality traits by individuals?
- (3) How does the collection of personalities influence group function and the interactions between group members?

Questions 1 and 2 consider the interaction between sociality and personality at the level of the individual, while question 3 explores effects at the level of the group, taking in work on social organisation and patterns of interactions between personality types, leadership, and the relationship between personality and producer-scrounger roles.

Our third aim is to identify general patterns in the findings of these studies, and highlight areas of focus for future work in order to develop our understanding of the relationship between personality and social context.

In considering social groups, we focus upon what we term ‘free-entry’ groups, where individuals are free to join and are accepted into whichever group they choose thus creating highly dynamic ‘fission-fusion’ societies. Many species form such groups, characterised by variable and context-dependent group size, low group fidelity and frequent exchange of individuals between groups (e.g. Croft *et al.*, 2003; Hoare *et al.*, 2004; Ward *et al.*, 2002). In reality, many free-entry groups may also contain more stable elements, such as bonded pairs of mates, or parents and offspring. These stable elements are considered in question 2, below, which focuses upon the relationships among group-mate identity, group composition and individual behaviour. We do not include what we term ‘restricted-entry’ groups, in which members generally exhibit high group fidelity, which are often hierarchically structured and from which existing group members actively repel and exclude would-be joiners. Restricted-entry groups are often kin-structured groups formed to defend territories or cooperatively forage or hunt, or harems. These fall outside the scope of this review, although it is possible that many of the issues considered here may also apply.

II. SOCIAL INFLUENCES UPON INDIVIDUAL BEHAVIOUR

(1) Conformity

Conformity describes the positively frequency dependent tendency of individuals to adopt the behaviour of the majority of their group mates, or of their near neighbours within the group, such that they become disproportionately more likely to perform a behaviour as the proportion of others performing it increases (Efferson *et al.* 2008). Conforming to the behaviour of others can influence how an individual interacts with its environment in a number of ways, for example by determining routes of travel, area occupancy, the timing and location of foraging and the types of food that are foraged for. Conformity may be especially important for species which gain anti-predator benefits from grouping. Predators exert substantial pressure against phenotypic and behavioural heterogeneity within groups, by disproportionately targeting odd individuals whose appearance or actions differ from those of the majority (Landeau & Terborgh, 1986; Ohguchi, 1978). Conformity may operate through simple local rules, through which,

for example, individuals align with their neighbours and attend closely to their behaviour, producing a high degree of behavioural uniformity amongst group members (Couzin & Krause, 2003; Couzin *et al.*, 2002).

There are numerous examples of conformity influencing the behaviour of social animals. Naive guppies (*Poecilia reticulata*) followed experienced group-mates on long, energetically costly routes to food patches, even when shorter alternatives were available (Laland & Williams, 1998). Individual three-spined sticklebacks (*Gasterosteus aculeatus*) tended to forage with larger shoals, even when doing so meant foraging in areas they had previously experienced to be relatively poor feeding grounds (Webster & Hart, 2006). Similarly, nutmeg mannikins (*Lonchura punctulata*) that had previously found one feeding area to be reliably productive switched to a less profitable feeding area after they saw others using it (Rieucou & Giraldeau, 2009).

Couzin *et al.* (2002) used simulation models to investigate the effects of changing the conformity rules governing local interactions between individuals and their immediate neighbours upon the properties and structure of the group as a whole. They found that by manipulating variables such as the degree to which individuals were attracted to and moved towards their neighbours, the degree and rate at which they turned to match their orientation, the volume of the zone in which they perceived and responded to their neighbours and the speed at which they travelled, they were able to produce groups whose global properties closely matched those seen in naturally occurring animal groups. Thus conformity and adherence to simple local rules governing spatial positioning and orientation relative to neighbours can have a strong homogenising effect upon the behaviour of group-living individuals. Through such rules the presence of group members may result in individuals behaving substantially differently than they would if they were acting independently of any social influence.

Conformity might affect the extent to which individuals within groups express personality traits in a number of different ways. For example it might cause individuals, whose personalities differ when acting alone, to converge on some common rate of expression. There may be a skew effect, with certain individuals in the group adopting the behaviour of the most- or least-responsive individuals, such that all individuals will not be affected equally. Fig. 1 depicts several plausible conformity effects scenarios. In principle it should be possible to identify these and similar conformity effects experimentally where they operate in animal groups, and such work could yield valuable insights. In Section III, we discuss some of these scenarios in relation to the findings of a number of studies that have specifically looked at the influence of the presence of group mates upon individual behaviour.

(2) Social facilitation

Social facilitation occurs when the presence of group mates affects the behaviour of an individual, allowing or causing them to engage in certain behaviours at a different rate, or

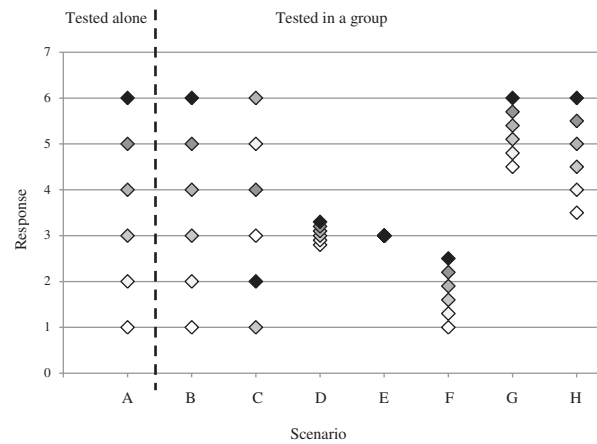


Fig. 1. A non-exhaustive list of possible scenarios describing the effects of conformity processes upon individual personality when individuals group together. Each point represents a different individual. Response refers to a continuous arbitrary score for some repeatable behavioural personality trait, with high-scoring ‘more responsive’ individuals engaging in the behaviour to a greater extent than low-scoring ‘less responsive’ ones. Note that for simplicity and clarity we have depicted individual response scores as being discreet, non-overlapping and equally spaced. In reality we might expect to see a normal or skewed distribution of scores. Scenario A shows baselines scores, obtained for individuals tested alone and free from any social influence. B shows a ‘null scenario’ in which there is no effect of being in a group upon individual scores. C shows a scenario in which there is no conformity effect, but where individual scores change such that behaviour when alone does not predict behaviour when embedded in a group. D shows a conformity scenario in which the responses of the individuals converge on the ‘mean’ response of the group. E describes a scenario in which conformity effects lead to identical responses in all individuals, completely obscuring the individual differences seen when tested alone. F and G depict scenarios in which the responses of most individuals are changed, with conformity pushing behaviour towards that of the least or most responsive individuals respectively. Finally, H describes a scenario where an individual at the responsive extreme remains unchanged, and entrains the responses of the others. In this example there is a bias towards the response of the most responsive individual, with increasingly less responsive individuals being more strongly affected. Note that the maximum and minimum response scores remain bounded by the original upper and lower values seen in Scenario A, when the individuals were tested alone. Conformity does not enhance or decrease responses beyond these bounds, as does facilitation (see Fig. 2 and main text).

to perform behaviours that they would not perform at all if they were alone (Zajonc, 1965). The proximate mechanisms driving social facilitation may include reduced perception of risk, decreased investment in vigilance or increased levels of competition.

Individuals in larger groups obtain greater anti-predator benefits than those in smaller groups, or singletons through improvements in collective vigilance as well as risk dilution, predator confusion and attack abatement (reviewed by Krause & Ruxton, 2002). These well-documented reductions

in *per capita* risk associated with group membership can allow individuals to reduce investment in threat-sensitive behaviours such as refuging or prolonged vigilance, enabling them to spend more time engaged in other, more profitable activities instead, such as foraging or courtship, and also potentially to exploit a greater range of habitat (Lima & Dill, 1990).

Socially-induced changes in individual behaviour, particularly increases in behaviours associated with resource exploitation can also be brought about by increased competition (Grand & Dill, 1999). This can cause individuals to alter the way that they trade-off between food intake rate and vigilance for threats. These proximate mechanisms may sometimes operate in tandem; individuals must change their behaviour in the presence of increasing numbers of competitors if they are to maintain a minimum level of resource intake, and are able to do so because increasing group size leads to decreased predation risk. The relationship between group size and changes in individual vigilance behaviour, along with the underlying causal mechanisms, are reviewed by Beauchamp (2003).

Facilitation effects can have a number of functional outcomes, for example by causing an individual to become more active, to travel greater distances, to spend more time in certain areas of habitat, to increase foraging and feeding rate or to become more likely to sample new types of resource. Facilitation may also cause individuals to decrease the rate at which they perform certain behaviours. Most obviously this may include anti-predatory behaviours, the rate of performance of which may be inversely proportional to the rate of performance of other non-compatible behaviours such as feeding or courting. The presence of others may also provide scrounging opportunities, which might cause a decrease in sampling or foraging in some individuals (Giraldeau & Caraco, 2000). This is relevant since vigilance and other behaviours associated with risk reduction are important components of some personality assays (reviewed by Reale *et al.*, 2007), while the relationship between personality and producer-scrounger roles is receiving increasing attention (e.g. Kurvers *et al.*, 2010a, discussed later on in this review).

Examples of facilitation effects on individual behaviour include the following: in the subsocial beetle *Odontotaenius floridanus*, males transported more eggs and both males and females travelled more rapidly when in groups compared to when alone (Punzo, 2007). Tadpoles of common toads (*Bufo bufo*) were more active in groups than when alone (Griffiths & Foster, 1998), rooks (*Corvus frugilegus*) increased their feeding rates when paired with a conspecific than when alone (Dally, Clayton & Emery, 2008) and walleye pollock (*Theragra chalcogramma*) visited more food patches when in groups than when alone (Baird, Ryer & Olla, 1991). In each case the ultimate outcome, an increase in activity and/or feeding or other behaviours of the focal individuals, can probably be ascribed to proximate mechanisms such as decreased perceived risk and investment in vigilance, or

increased competition, or a combination of both, as discussed above.

As with conformity, facilitation effects may affect the ways in which individuals within groups express personality traits in a number of different ways. In some cases all individuals might increase their behaviour by the same degree, such that while the rate of expression changes, individual relative differences (seen when the animals are tested or observed when alone and free of social influence) are preserved. In other cases individuals might be affected differently; individuals at the behavioural extremes might be affected to a lesser or greater degree, or may entrain the behaviours of others, for example. This may or may not affect individual relative differences; in extreme cases all individuals might converge on a common rate of expression. Several possible facilitation scenarios are presented in Fig. 2. As with the conformity scenarios discussed above, many of these facilitation scenarios can be investigated and identified experimentally, and we discuss below some of them in relation to the findings of a number of studies that have specifically looked at the influence of sociality upon individual behaviour (Section III).

Contagion (or contagious behaviour) is another social influence upon individual behaviour. While the terms 'contagion' and 'social facilitation' have sometimes been used interchangeably in the past, by the definitions of Galef (1988) and Nicol (1995) they are separate and distinct processes. Contagion describes the process by which the behaviour of one or more individuals induces other individuals within the group to perform that same behaviour. Note that in social facilitation, the affected individual changes its behaviour when in the presence of others, but does not necessarily have to perform the same behaviour as its group mates. It seems reasonable to assume that personality might determine the extent to which individuals are influenced by contagion, however to our knowledge this has not been previously investigated. Compared to social facilitation, contagion has received little empirical attention. Nicol (1995, and references therein) provides possible examples of contagion in animals.

III. EMPIRICAL INVESTIGATIONS OF PERSONALITY AND SOCIAL CONTEXT

The preceding section demonstrates how conformity and social facilitation can act upon the behaviour of individuals. Here we consider studies that have specifically looked at the influence of sociality upon individual behaviour. These are arranged under three questions that together explore the interaction between sociality and personality at the level of the individual (questions 1 and 2), and at the level of the group (question 3).

In detailing the behaviours covered in these studies we have referred to the specific assay or response variable used in the study (such as 'latency to recover from fright stimulus') rather than using general terms such as 'bold' or 'shy'. While this is sometimes cumbersome, we feel that it is preferable

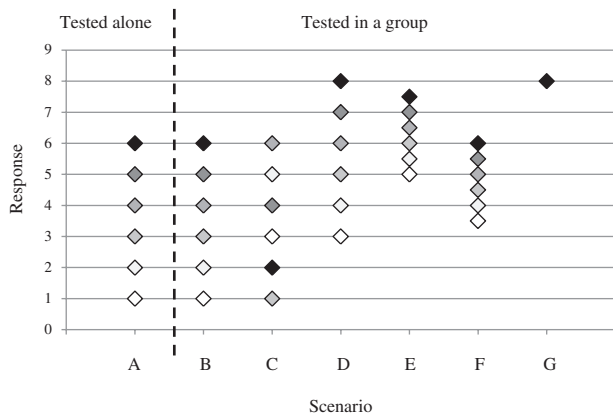


Fig. 2. A non-exhaustive list of possible scenarios describing the effects of facilitation effects upon individual personality when individuals group together. Each point represents a different individual. Response refers to a continuous arbitrary score for some repeatable behavioural personality trait, with high-scoring 'more responsive' individuals engaging in the behaviour to a greater extent than low-scoring 'less responsive' ones. Note that for simplicity and clarity we have depicted individual response scores as being discreet, non-overlapping and equally spaced. In reality we might expect to see a normal or skewed distribution of scores. Scenario A shows baseline scores, obtained for individuals tested alone and free from any social influence. B shows a 'null scenario' in which there is no effect of being in a group upon individual scores. C shows a scenario in which there is no facilitation effect, but where individual scores change such that behaviour when alone does not predict behaviour when embedded in a group. In D-G we have used examples where facilitation effects cause individuals to increase their responses. In some instances we may expect to see a decrease in behavioural responses brought about by facilitation, for example in behaviours associated with reducing predation risk such as hiding, freezing or maintaining vigilance. D represents a scenario where all individuals are affected by facilitation to the same degree. E shows a scenario in which all individuals are affected, but not equally; in this example less responsive individuals are affected to a greater degree than more responsive ones. In scenario F not all individuals are affected; in this case the more responsive individuals do not increase their response and only the less responsive ones are affected. G describes a scenario in which conformity effects lead to identical responses in all individuals, completely obscuring the individual differences seen when tested alone. Note that the outcome of F here is the same as that of the conformity scenario G (Fig. 1). In experimental investigations it may sometimes be difficult to separate conformity and facilitation effects.

as it avoids ambiguity of terminology, a problem highlighted by previous reviews of the field (e.g. Reale *et al.*, 2007).

(1) Question 1: is individual variation for a given personality trait expressed consistently between asocial and social contexts?

Numerous studies have explored a variety of personality traits in a diverse range of species in order to gain insight into the potential roles played by these axes of variation

in ecological and evolutionary processes. However, many of these have tested in isolation individuals of species that are at least facultatively social. It is therefore critical to determine whether behaviour when tested alone corresponds to behaviour when interacting with conspecifics (see Figs 1 and 2). Most broadly, it is necessary to investigate whether social context affects individual personality at all, or whether personality is expressed independently of the presence of others. If animal personality is indeed influenced by social context, then this raises a series of questions. In the first instance, we need to determine broadly the nature of this influence by asking questions such as: can individual behavioural responses manifested in an asocial context predict those seen while grouping with others? Is the rank order of the behavioural responses of a set of individuals comparable when tested alone and while grouping? Subsequently, we need to determine whether the social influence produces a predictable, directional response on individual behaviour, for example: are behavioural responses enhanced or suppressed? Can facilitation and conformity effects operate simultaneously, and are some behavioural types affected more than others? To date, only a few investigations have addressed the issue of individual responses in asocial and social contexts, and many of these questions remain unexplored. Below we review the findings of several studies in this area.

van Oers, Klunder & Drent (2005b) quantified exploratory behaviour in male and female great tits (*Parus major*) and investigated the relationship between this trait and their latency to resume feeding following a startle response. The latter measure was conducted both in the absence and then the presence of a conspecific, providing a social context. Females tended to resume foraging later when the conspecific was present, irrespective of their exploratory tendency or the behaviour of the conspecific. Males tended to resume foraging sooner when the conspecific was present, compared to when tested alone, but individuals that explored more slowly were seen to have a lower latency to return when the conspecific was present, suggesting a directional facilitation effect upon personality, affecting slower, but not faster explorers (similar to scenario F in Fig. 2).

Webster, Ward & Hart (2007) looked at three measures of behavioural variation in three-spined sticklebacks: the ability of focal fish within a group to compete for prey, activity in a novel environment and latency to resume foraging after a simulated predator attack. To obtain the latter two measures the focal fish was tested alone. These behaviours were found to be correlated - fish that were more active were seen both to be better competitors (based on prey share won) and to resume foraging sooner following disturbance. Furthermore they saw that fish which were more active and which resumed foraging sooner tended to obtain a larger prey share both in groups of two and in groups of six. Next they looked at group-size effects upon activity and latency to resume foraging. One set of fish were tested while alone in both contexts, and their behavioural responses were seen to be correlated between contexts, as before. In a second and a third set, fish were

tested alone in either the activity test or the latency to resume foraging test but within a group in the other test. Here no correlation between the responses of individuals was seen. Testing of either behaviour in the presence of conspecifics was sufficient to uncouple these responses. Furthermore, median activity rates were higher and latency scores lower for focal fish tested in groups compared to those tested alone. This suggests facilitation, with an effect similar to those described in scenarios F or G in Fig. 2.

Magnhagen & Bunnefeld (2009) investigated the effects of social context upon risk-taking behaviour in individual perch (*Perca fluviatilis*). Risk taking was assayed by quantifying time spent in open water feeding in sight of a predator and time spent in a refuge, a patch of vegetation. Focal fish tended to behave more boldly when in a group, spending more time in open water compared to when they were alone. Correspondingly, bolder fish showed the smallest change in response variable scores when in groups compared to when alone. Also, variation among individuals was greater when they were tested alone, indicating greater dispersion of response variable scores. This suggests that sociality may to an extent restrict diversity in individual responses. Interestingly, individual responses were nevertheless seen to be positively correlated between alone and group exposures, suggesting that for perch, individual behavioural traits may still be expressed within groups, despite this dampening effect. Again this finding may be due to facilitation effects, such as those described in scenarios E or F in Fig. 2, while conformity, with greater influence of more responsive individuals may also play a role (scenarios F and G in Fig. 1).

Schuett & Dall (2009) investigated the relationship between individual variation in solitary and social exploratory behaviour in male and female zebra finches (*Taeniopygia guttata*) and their performance in foraging trials when placed in mixed-sex pairs. While males were not more exploratory than females, they were seen to be more consistent in the expression of exploratory behaviour. When tested in pairs, it was seen that the behaviour of an individual was influenced by that of its partner; birds paired with a more exploratory partner were seen to be more exploratory themselves relative to their behaviour when tested alone.

Taken together, these studies demonstrate a complex and context-dependent influence of sociality upon individual behaviour. They reveal that in some instances, different behavioural responses that are correlated when individuals are tested alone become uncoupled when they are tested in the presence of conspecifics in either one of the exposures. In the case of Webster *et al.*'s (2007) threespine sticklebacks, this may be attributed to the influence of social facilitation effects in the case of latency to resume foraging and perhaps a combination of social facilitation and conformity in the case of activity. In other instances, even though individual behaviour can be affected markedly by the presence of group mates, individual variation can nevertheless persist such that behaviour expressed alone and within a group remain correlated (Magnhagen & Bunnefeld, 2009). Finally, both van Oers *et al.* (2005b) and Schuett & Dall (2009) also

detected sex differences in the effect of social context upon behavioural consistency.

Clearly, there is much work to be done in answering this question. One major issue that has so far not been addressed relates to group size and density-dependent effects. Many behavioural responses are known to be strongly influenced by the number of group mates present (Krause & Ruxton, 2002). While the studies outlined above have shown that the behaviour of focal individuals is changed, albeit in a number of different ways, by the presence of one or more group mates, it is not clear what the effects of increasing numbers of group mates might have upon these behavioural changes. Furthermore, for many of the model species used in behavioural ecology, naturally occurring group sizes may be much larger, sometimes up to one or two orders of magnitude greater, than those used in experimental studies. The influence of conformity might exclude many aspects of individual behavioural variation in larger groups, for example in flocks of starlings (Ballerini *et al.*, 2008), swarms of locusts (Buhl *et al.*, 2006) or shoals of fish (Radakov, 1973) and we return to this point in the final section of the review. The behavioural reaction norm approach advocated by Dingemanse *et al.* (2010) represents a useful means of investigating these effects.

(2) Question 2: does group mate identity and the composition of the social group influence the expression of personality traits by individuals?

While the behaviour of individuals can be affected by the mere presence of group mates, through facilitation or conformity, there may also be an influence of traits particular to their group mates themselves, adding a further layer of complexity. This may relate to their sex or phenotype, the relationship between individuals, as well as group-mate personality.

Sih & Watters (2005) looked at the effects of group composition on male mating success in water striders (*Aquarius remigis*). Specifically they ranked males according to a score which combined their activity levels and aggressive responses and formed them into groups of descending activity and aggression, such that the mean behaviour type of each group differed but within-group variance was low. These groups had access to females, and individual- and group-level male mating success was quantified for each group. They saw that male mating success was highest in the groups of intermediate active-aggressive behaviour type. Individuals in the groups of the most active and aggressive males had the effect of driving the females into refuge. The authors argue that the presence of certain keystone individuals within the group can indirectly determine the success of other group members. While the behavioural type of a given individual may predict its mating success, there is also a substantial influence of the behavioural types of its group mates in general and of certain influential individuals in particular.

Harvey & Freeberg (2007) investigated whether changes in the social environment altered the expression of a range of behaviours in male-female pairs of Carolina chickadees

(*Poecile carolinensis*). Birds were captured from the wild and males and females from the same flock were paired in the laboratory. Pairs were held together for several weeks, before the male from each pair was swapped with the male from a different pair. Individuals within each pair were assayed multiple times both before and after the switch was made. They saw that the expression of behaviours including aggression, dominance and rate of vocalisation remained consistent within individuals even after their partner had been switched. There was little evidence of sex differences. The authors suggest that the traits measured are relatively fixed within individuals and show little plasticity in response to changing social structure, albeit when the social structure in question concerns only two animals.

Piyapong *et al.* (2010) found an interaction between sex and group composition in guppies (*Poecilia reticulata*). Focussing upon latency to resume activity following a simulated predator attack, they saw that focal individuals of both sexes resumed activity more rapidly when grouped with males than with females. Males may take longer to resume activity in the presence of females because they are more conspicuous in general and perhaps are more likely to be targeted by predators due to oddity effects. Females may become active sooner when shoaling with males in order to reduce the costs of receiving sexual harassment, which can include increased predation risk (Pocklington & Dill, 1995), reduced foraging rate (Magurran & Seghers, 1994), and forced copulations that undermine female mate choice (Matthews & Magurran, 2000).

Other studies too have noted that the personality of group mates can affect the responses of others within the group including Magnhagen & Bunnefeld (2009), Schuett & Dall (2009) and van Oers *et al.* (2005b) discussed previously, and Harcourt *et al.* (2009) and Kurvers *et al.* (2009) discussed below in relation to leadership. Magnhagen & Staffan (2005) and Dyer *et al.* (2009) explored this idea explicitly by creating and studying groups that varied in the composition of their personality types.

Magnhagen & Staffan's investigation (2005) explored the effects of sociality upon individual use of open-water habitat and feeding activity in juvenile perch (*Perca fluviatilis*). Perch were first assigned at random to groups of four, and for each individual they recorded time spent in open habitat (and therefore out of refuge) and the number of prey attacks that it performed. Based upon their responses the fish were categorised into personality types: shy, bold or intermediate. They were then assigned to new groups, matched for personality category. They saw that in groups of shy fish (least time in open water and lowest feeding rate in the previous test) individuals showed the largest changes in behaviour, significantly increasing the time they spent in the open and the number of prey attacks they performed compared to when they were tested within groups composed of randomly assigned individuals. Bold individuals (most time in open water and highest feeding rate in the previous test) decreased their time in the open when in a group, whereas intermediate individuals did not alter their

behaviour according to the social context. This suggests that the behaviour of perch in the different personality categories is determined by their behavioural type but is also influenced by their group mates and by habituation to the testing environment. This conclusion was explicitly tested and supported in a further study by Oosten, Magnhagen & Hemelrijk (2010). This study used agent-based modelling to reveal that time spent in the open in the presence of a predator, one of the response variables quantified in Magnhagen & Staffan's (2005) empirical investigation, was influenced by both prey competition and social facilitation as well as habituation through previous experience. These parameters were sufficient to replicate the patterns of behaviour seen in Magnhagen & Staffan's (2005) original study both when the model contained groups of individuals whose boldness behaviour was initially identical and also when the individuals within groups all differed in their boldness.

Dyer *et al.* (2009) quantified latency to resume activity following a disturbance in guppies, and created shoals composed of fish that either all had a low latency, all had a high latency, or which contained a mixture of high- and low-latency fish. These were then tested in a foraging task. While the low-latency and mixed groups were fastest to find the feeding area, it was the mixed, and not the low-latency group that had the highest feeding rate. They argue that this was due to the fact that while low-latency fish were most likely to start feeding first in the mixed groups, they were almost always followed into the feeding areas by high-latency fish. It is possible that facilitation and/or conformity effects may influence low-latency fish to a lesser degree (since these fish were first to enter the foraging area and begin to feed) while acting more strongly upon high-latency fish, causing them to adopt the behaviour of the low-latency fish. In groups composed entirely of low-latency fish, individuals may be less attuned to social cues and hence less likely directly to follow others to the feeding area, while in groups of high-latency fish it is less likely that any individuals will enter the feeding area at all. In both cases this could result in a lower overall feeding rate.

Collectively, these studies suggest that a number of factors relating to group-mate sex and individual behavioural type can influence the behaviour of a given individual in a social context (but see Harvey & Freeberg, 2007). In particular, the composition of personality types within the group can feed back to affect both the behavioural responses of its constituent individuals and the way in which the group as a whole functions in relation to the environment.

(3) Question 3: how does the collection of personalities influence group function and the interactions among group members?

Following from the previous questions, which considered the effect of grouping and group composition upon the behaviour of the individual, we now ask how the composition of personality types affects the structure and dynamics of the group itself. First we ask whether personality

plays a role in determining social organisation, which has important implications for the transmission of information and pathogens among members, and may influence the distribution of competitive, reproductive and cooperative interactions within populations (Croft, James & Krause, 2008). We then ask how personality might influence leadership and group-level patterns of space use. Finally we ask whether personality determines tendency to copy others, and whether this predicts the adoption of producer-scrounger roles within groups. We review this work under three sub-headings, taking in social organisation, leadership and producer-scrounger behaviour.

(a) Social organisation

The organisation of groups determines the frequency and patterns of interactions among individuals, and has implications for the transmission of genes, pathogens, information, and novel behaviours through populations (Croft *et al.*, 2008). To date, very few studies have looked at the role of personality in determining social organisation. Using social network analyses, Pike *et al.* (2008) showed that three-spined sticklebacks that resumed feeding more rapidly following a startle stimulus tended to interact less regularly with others within their group but tended to distribute these interactions evenly among individuals. By contrast, fish that took longer to resume feeding were seen to interact more frequently but with a smaller subset of the same few individuals. Croft *et al.* (2009) looked at the relationship between individual tendency to inspect predators and to shoal in guppies and related these measures to individual connectivity measures in a social network of wild guppies. Predator inspection and shoaling tendencies were seen to be negatively correlated and did not differ between sexes. Fish that had a low tendency to inspect predators and a high tendency to shoal were seen to interact with a greater proportion of individuals within the study population and to associate with these individuals, on average, more frequently. This to an extent is at odds with the findings of Pike *et al.*'s (2008) study, where it was the 'bolder' fish that were seen to interact with the greater number of individuals, although this difference could be due to any number of differences between the species, the environment of the source population, the assays used and the experimental environment. Croft *et al.* (2009) looked at a wild, free-ranging population, an approach that allows groups to form naturally *via* self-organising processes. Social network analysis represents a powerful approach for determining the effects of personality upon group composition and social organisation and we discuss possible directions for further work in this area in Section IV.

(b) Leadership

An individual's spatial position within a group is one of the most important determinants of the costs and benefits that it receives from sociality. In stationary groups, arguably the most prominent spatial difference in terms of the cost-benefit relationship occurs between peripheral and central positions.

Empirical evidence exists to support Hamilton's 'selfish herd' theory (Hamilton, 1971) that in a stationary group, peripheral individuals are at a much higher risk of predation than those in central positions (Romey & Galbraith, 2008). In mobile groups, in addition to edge and centre, front and back positions are also associated with different costs and benefits, individuals at the front of groups are attacked significantly more than those in the centre or back of the group. Set against this, both food availability and food quality are higher at the front of mobile groups and the periphery of stationary ones, as the capture of food items by individuals at the front or edge limits the amount of food reaching the back or centre. The balance between these risks and rewards means that we should expect trade-offs between the costs and benefits of maintaining such high risk/high reward positions (Bumann, Krause & Rubenstein, 1997; Krause, 1994). Furthermore, individuals occupying front positions in moving groups are known to exert the greatest influence over the direction of travel of the group as a whole (Bumann & Krause, 1993), i.e. they act as leaders. The interaction between group geometry and leadership and personality therefore has important implications not only for individual fitness, but also for group functioning.

Ward *et al.* (2004) investigated the relationship between a number of behaviours in three-spined sticklebacks, finding that latency to resume foraging after a simulated predator attack was positively correlated with tendency to shoal. Individuals that had a low latency to resume foraging and a low shoaling tendency tended to be superior competitors for prey in a scramble competition environment. They also were more likely to assume a position towards the front of a shoal compared to high latency/high shoaling tendency fish.

Leblond & Reeb (2006) investigated leadership behaviour in shoals of golden shiners (*Notemigonus crysoleucas*). They found that within groups of 12 fish there were 1–3 individuals which consistently tended to occupy forward positions and to move at the head of the shoal. They saw that these front-position-occupying individuals exhibited a non-significant tendency ($P < 0.1$) to be more willing to pass through an opaque tube, but that they were no more likely to emerge from a refuge sooner than fish that occupied other shoal positions (passing through the tube and latency to emerge from refuge were both taken as measures of risk-taking, or exploratory behaviour).

Harcourt *et al.* (2009) quantified tendency to leave cover and search for food in open water, a potentially risky behaviour, in three-spined sticklebacks. From a pool of assayed fish they randomly paired individuals. While they found that each fish influenced the other—one was more likely to leave or return to cover if the other did so—they also saw that within pairs, fish which left cover most readily when tested alone were more likely to initiate leaving cover, and were less responsive to their partner's behaviour. Those fish within the pair that spent the least time in the open when tested alone were more likely to follow when paired and through positive social feedback processes elicited greater activity in open water in their partner.

Kurvers *et al.* (2009) investigated personality effects on leadership in barnacle geese (*Branta leucopsis*). For individuals tested alone, activity levels and neophobia scores were found to be strongly consistent over repeated exposures. When individuals were paired up in a social foraging task, it was seen that the least neophobic bird was more likely to lead its partner to the food patch.

Taken together, the studies of Ward *et al.* (2004), Harcourt *et al.* (2009) and Kurvers *et al.* (2009) suggest that tendency to lead, a potentially risky behaviour, but one that is also associated with potentially greater access to resources, is predicted by tendency to accept risk in other situations, namely latency to resume foraging after a disturbance, tendency to leave cover and tendency to interact with novel spaces or objects, respectively. The possibility that bold individuals consistently act as leaders while shy individuals act as followers, has significant implications for group dynamics. For example, if bold individuals drive group behaviour, then this is likely to place pressure upon shy individuals to conform to the bold phenotype, since a failure to do so could result in separation from the group and a loss of the benefits of sociality. Moreover, recent research suggests that the geometrical relationship between bold and shy individuals within groups may deliver important benefits, particularly in terms of foraging, which we explore in the following section.

(c) *Producer-scrounger interactions*

The acquisition of information from social sources, by monitoring or interacting with others, or *via* private exploration of the environment is thought to be associated with a range of costs and benefits. In many animals, foraging and maintaining vigilance for predators are mutually exclusive actions; individuals that have their heads down as they graze, subdue prey, or search for food are unable to scan for predators, and may be less likely to detect them as they approach (e.g. Coolen & Giraldeau, 2003). Furthermore, predators may preferentially target prey assuming feeding postures, in order to capitalise upon their unwariness (Krause & Godin, 1996). For this reason many animals adopt scrounger tactics, monitoring the foraging behaviour of others within their group rather than searching for prey directly themselves (Giraldeau & Caraco, 2000), or else watching others from cover (e.g. Coolen *et al.*, 2003), and either joining them or subsequently visiting areas at which they have discovered prey. Individuals can adopt both producer and scrounger roles interchangeably (Giraldeau & Caraco, 2000) and are known to switch between different sources of information in changeable environments in order to maximise their benefits (e.g. Webster & Laland, 2008). The idea that personality traits might predict relative reliance upon private and social sources of information and the adoption of producer or scrounger tactics has received attention in several recent studies.

Marchetti & Drent (2000) identified consistent differences in speed of exploration in great tits (*Parus major*) and divided these into two groups of faster and slower explorers. These were trained to feed from one kind of feeder, and were then

tested, once alone and once with a demonstrator that was trained to feed at a different type of feeder. When tested alone and in the absence of food, the slow explorers were seen to be more likely to extend their search to other feeders while fast explorers continued only to visit the feeders to which they were trained. However, when a demonstrator was present slow explorers did not change their behaviour compared to when they were alone, while fast explorers visited the demonstrated feeder significantly more often, suggesting scrounging behaviour.

Webster *et al.* (2007) tested whether three-spined sticklebacks were able to use social information from two equally sized groups of fish feeding from patches that yielded prey at different rates. The patches were designed so that the tested fish could not see the prey but could estimate patch yield based upon the feeding behaviour of the attendant conspecifics. These fish were also individually assayed for activity in a novel environment and latency to resume foraging after a simulated predator attack. While they saw that most of the tested fish were able to select the richer feeding patch based upon the prey-capture behaviour of the attendant shoal, individual tendency to approach and join the shoal feeding at the higher quality prey patch was not related to either individual activity or latency to resume foraging.

Also working with three-spined sticklebacks, Harcourt *et al.* (2010) investigated whether boldness was related to the use of three different categories of social information, social cues, local enhancement and public information. In this study fish were categorised as either bold or shy based upon the amount of time they spent out of cover, and individual boldness was seen to be expressed consistently between trials. In the social cues assay the focal fish was allowed to observe a large and a small shoal held at either end of a test tank. These were then removed and the focal fish was allowed to move into the areas where it had seen the shoals. In the local-enhancement treatment the focal fish was given the opportunity to move into the areas where it had seen two equally sized shoals, one of which had been feeding while the other had not. Finally, in the public-information treatment both groups were allowed to feed, but at different rates and the focal fish was then allowed to move into the areas where it had seen them, as before. The tested fish responded to both social cues and local enhancement, preferring the areas where they had seen the larger of two groups and the area where they had seen one group feeding. They did not respond to public information however, suggesting that they could discriminate absolute but not relative differences in conspecific feeding rates. As in Webster *et al.* (2007), differences in focal fish boldness were not seen to be related to information use. However, Harcourt *et al.*'s (2010) study did reveal that the time taken to select an area differed between boldness categories, with shy fish (those that spent the least time in open water) taking longer and exhibiting the greatest variation in latency to select an area. This suggests that personality may play an indirect role in determining how individuals of some species act upon social information.

Dyer *et al.* (2009) created shoals of guppies which contained a mixture of fish with high or low latencies to resume activity following a disturbance. Within these groups, low-latency fish were significantly more likely to enter a feeding area and begin to feed first, and a high-latency fish was more likely to be the second to feed, which could be indicative of a producer-scrounger relationship between the two behavioural types (see above).

Kurvers *et al.* (2010a) investigated producer-scrounger behaviour in barnacle geese as a function of neophobia. They found that neophobic reactions measured in two different tests were expressed consistently across individuals. They went on to show that in group foraging trials, less-neophobic individuals were more likely to discover food patches, while more-neophobic individuals were more likely to join others at already discovered patches. A second study (Kurvers *et al.*, 2010b) showed that neophobia scores were also positively correlated with use of social information in a binary choice experiment. Geese that were more neophobic were more likely to approach an area where other geese were feeding relative to an area where other geese were present but were not feeding.

The studies by Marchetti & Drent (2000), Dyer *et al.* (2009) and Kurvers *et al.* (2010a,b) suggest that personality might play a role in determining producer-scrounger roles in some animal groups. This is perhaps unsurprising, given that personality (and specifically boldness) has been shown to govern tendency to accept risk across a range of different contexts. In this context risk is associated with engaging in foraging at the expense of mutually incompatible, or less-effective vigilance for predators. The two studies in three-spined sticklebacks however (Webster *et al.*, 2007; Harcourt *et al.*, 2010), revealed no direct relationship between personality scores and scrounging or social information use. It seems likely that such relationships may be species or context specific, highlighting the need for caution when comparing findings and seeking general patterns or relationships from experimental studies. Further work could consider the relationship between personality and the tendency to gather and use social *versus* private information when the two are in conflict or when the costs associated with using either differ, and we discuss this below.

IV. SUMMARY AND DIRECTIONS FOR FUTURE RESEARCH

The preceding review of experimental studies investigating the relationship between individual personality and sociality reveals the often complex nature of the influence of sociality and social processes upon the expression of personality by individuals, and also the influence of the collection of personality types upon the structure of and patterns of interaction within social groups. On the one hand, these studies have shown that the behavioural responses constituting 'personality' seen in individuals when tested alone can change markedly when tested again in a social

context. In one study (Webster *et al.*, 2007) two behaviours that were correlated in individuals tested alone became uncoupled when they were tested with conspecifics in one assay. In another study however (Magnhagen & Bunnefeld, 2009), it was seen that even though the presence of group mates significantly affected individual behaviour compared to when alone, individual behavioural responses remained predictable across asocial and social contexts. The degree of change induced by the presence of conspecifics on the responses of individuals compared to when alone is also influenced by the initial responsiveness of the individual (its location on the axis or continuum of the behavioural trait in question) and also its sex (Magnhagen & Bunnefeld, 2009; Schuett & Dall, 2009; van Oers *et al.*, 2005b). Factors specific to the group mates themselves were also shown to influence the personality measures of the focal animal. These included their sex (Piyapong *et al.*, 2010) as well as their own personality types (Dyer *et al.*, 2009; Magnhagen & Staffan, 2005). Finally, looking at the importance of the collection of individual personality types upon the dynamics of the group as a whole, it is clear that personality can influence patterns of interaction in social networks (Croft *et al.*, 2009; Pike *et al.*, 2008), leadership (Harcourt *et al.*, 2009; Kurvers *et al.*, 2009; Ward *et al.*, 2004) and producer-scrounger interactions (Dyer *et al.*, 2009; Kurvers *et al.*, 2010a; Marchetti & Drent, 2000). Throughout the review we have highlighted specific areas which we suggest merit further investigation, and we expand upon these below.

(1) Group size and density effects

While we have reviewed a number of studies that have tested the effects of the presence of group mates upon individual personality, to date no study that we are aware of has investigated how the individual behavioural responses comprising personality change as a function of increasing group size or density. This is vitally important if we are to have a fuller understanding of the significance of individual behavioural variation under natural conditions. The strength or influence of conformity and facilitation effects can increase with increasing group size or density and many behavioural responses are known to be density dependent (e.g. Palestis & Burger, 1998). Many of the model species commonly used in behavioural ecology, including research into personality, often occur in group sizes that are far larger than those commonly used in experimental studies.

In Fig. 3 we consider some scenarios of the effects of increasing group size upon the expression of responses and overall inter-individual variability for a given arbitrary personality measure within the group. These range from linear and non-linear facilitation effects, which may serve to increase responsiveness in some or all individuals, and conformity effects which drive more- and less-responsive individuals towards some common response level, decreasing the overall range or diversity of personality response measures as group size increases. It also considers threshold response changes, with individuals changing response levels only after some critical group size or density is reached, and more

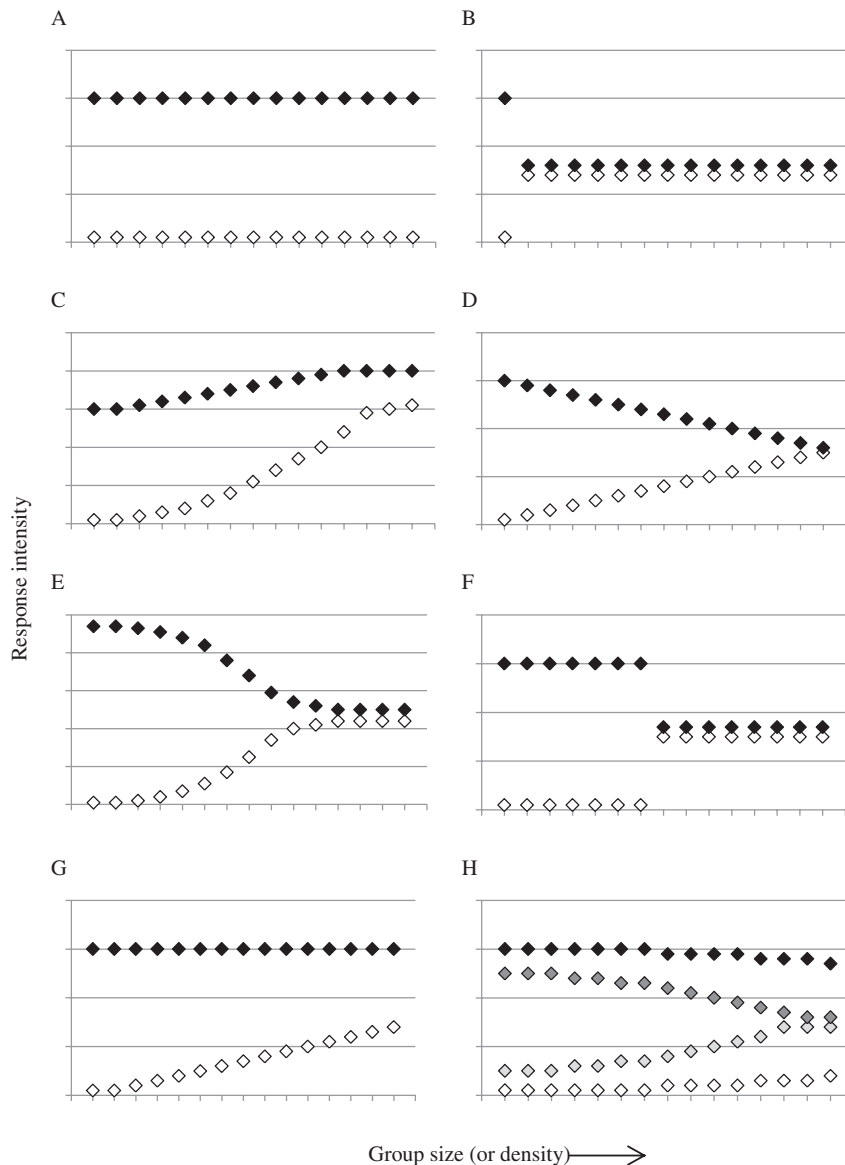


Fig. 3. Some scenarios of the effects of group and/or density size upon variation in behavioural responses. The first interval on the x axis corresponds to a group size of 1, representing individuals tested in isolation. The black and white points respectively show the behaviour of the most and least extreme expressers of the personality trait within the group. (A) A scenario of no effect; the most and least responsive individuals do not change their behaviour as group size increases. (B) An immediate effect of grouping with others, with individuals adopting a common response level as soon as they group with others. (C) Strengthening facilitation effects with increasing group size. (D, E) A linear (D) and non-linear (E) conformity-led transition to a common response level. (F) A threshold response, in this case through conformity processes, with individuals adopting a common response level only after some critical group size or density is reached. (G) A scenario in which individuals at different ends of the response spectrum are affected differently; in this case less responsive individuals are affected to a greater extent. (H) An example of a more complex scenario in which individuals with initially differing response levels are affected differently by increasing group size or density. Here the extreme individuals change little, while intermediately scoring individuals are affected to a greater degree. Group size or density dependent-effects could be brought about through both conformity and facilitation process, described in Figs. 1 and 2.

complex scenarios in which individuals with initially differing response levels are affected differently by increasing group size or density. This list of scenarios is non-exhaustive, and it is possible that some of the effects described in the scenarios may act in concert. In principle it should be possible to search for such effects by fitting appropriate

models to data obtained from well-designed experiments. Some basic questions that might be addressed by such an approach include: is there a density-dependence effect on the expression of personality, and if so, what is its nature? And, are some personality types affected more than others as group size or density changes? Dingemanse *et al.*'s

(2010) behavioural reaction norm approach could be used to study such changes in individual behaviour over gradients of group size, density or composition. Also, we might ask, do these effects differ between obligate and facultatively social species, where we might also expect to see lower variation in personality measures in the former than the latter, even when tested alone? This last question attempts to make a general link between personality and the breadth of inter-individual variation and population- and species-level sociality. Such a question could be tackled through a comparative approach, comparing populations, closely related species or ecologically similar species that are known to differ in their sociality, or possibly also through meta-analyses.

Recent work on collective behaviour (Sumpter *et al.*, 2008; Ward *et al.*, 2008) has shown that behaviours such as group movements between different areas of habitat can be initiated by a minority of individuals and subsequently adopted by others. This research has highlighted the importance of quorum rules, where the probability of undecided or uninformed individuals taking a given course of action increases non-linearly with the number of individuals that have already taken that action. Often the threshold number for such a quorum response is low relative to the overall group size, suggesting the possibility that collective decision-making processes could be dominated by a subgroup of individuals. While several studies have revealed how personality might determine the likelihood of an individual performing a behaviour such as initiating a movement, and the likelihood of observing individuals copying it (Dyer *et al.*, 2009; Harcourt *et al.*, 2009; Kurvers *et al.*, 2009), as yet the role of animal personality in collective decision-making remains largely unexplored. It is perhaps feasible to suggest that decisive, potentially bold, individuals may play a central role and this may prove a fruitful avenue for empirical studies.

(2) Social organisation

To date only two studies have offered an insight into the relationship between personality and social organisation (Croft *et al.*, 2009; Pike *et al.*, 2008) and there is scope for much interesting work in this area. Social network analysis represents a powerful approach for determining the effects of personality upon group composition and social structure, and laboratory, mesocosm and field studies in this area would be useful. Important questions that could be addressed include: are personality types distributed evenly throughout groups or are groups assorted according to personality? Where assortment by personality type is seen, is this a passive consequence, arising for example from differences in where and when different personality types are active, or from differences in group size preferences, or is it a consequence of active social preference and discrimination by individuals? Does the distribution, relative abundance or range of different personality types differ among populations as a function of differences in ecological factors such as predation risk, food distribution or population density? Relating personality to social organisation in free-ranging

populations will better enable us to understand the functions and trade-offs associated with different personality types.

(3) Producer-scrounger interactions, information use and learning strategies

Research by Marchetti & Drent (2000), Dyer *et al.* (2009) and Kurvers *et al.* (2010a,b) linked personality type to producer-scrounger roles. As discussed above, this may be unsurprising, since boldness determines tendency to accept risk across a range of different contexts, which may include a greater investment in searching for and sampling resources at the expense of mutually incompatible, or less effective vigilance for predators. Theoretical work on social learning and information use predicts that individuals should be selective about when and who to copy (Laland, 2004; Laland *et al.*, in press). This work considers who individuals should copy (such as kin, successful individuals, the majority) and when they should copy (such as when privately held information is incomplete or outdated, when the costs of being wrong are high, when gathering new information is costly, or when the environment is subject to rapid or unpredictable change), and makes testable predictions about what individuals should do when different sources of information available to them conflict. We know of no studies to date which have investigated whether any facet of personality is related to how individuals weight different sources of information when they are in conflict and there is much scope for integrating work on social learning strategies and personality.

V. CONCLUSIONS

- (1) Social context has clear quantitative and qualitative effects upon the expression of personality traits by individuals. These should be accounted for in future studies of animal personality.
- (2) Personality can affect interactions among individuals within groups, determining social network structure, as well as influencing individual propensity to lead or follow, and produce or scrounge.
- (3) Existing data provides only a tentative insight into the relationship between personality and social context. We have at present little information on the effects of group size and density upon personality, and only a limited understanding of the relationship between personality and social organisation and information use. These areas are ripe for further research.

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