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Review

Evolutionary causes and consequences of consistent individual variation in cooperative behaviour

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Behaviour is typically regarded as among the most flexible of animal phenotypic traits. In particular, expression of cooperative behaviour is often assumed to be conditional upon the behaviours of others. This flexibility is a key component of many hypothesized mechanisms favouring the evolution of cooperative behaviour. However, evidence shows that cooperative behaviours are often less flexible than expected and that, in many species, individuals show consistent differences in the amount and type of cooperative and non-cooperative behaviours displayed. This phenomenon is known as ‘animal personality’ or a ‘behavioural syndrome’. Animal personality is evolutionarily relevant, as it typically shows heritable variation and can entail fitness consequences, and hence, is subject to evolutionary change. Here, we review the empirical evidence for individual variation in cooperative behaviour across taxa, we examine the evolutionary processes that have been invoked to explain the existence of individual variation in cooperative behaviour and we discuss the consequences of consistent individual differences on the evolutionary stability of cooperation. We highlight that consistent individual variation in cooperativeness can both stabilize or disrupt cooperation in populations. We conclude that recognizing the existence of consistent individual differences in cooperativeness is essential for an understanding of the evolution and prevalence of cooperation.

Keywords: cooperation; altruism; animal personality; behavioural syndrome; phenotypic plasticity

1. INTRODUCTION

Individuals often vary consistently in their behavioural responses to challenges, a phenomenon that has been termed ‘animal personality’ (Gosling 2001; Drent *et al.* 2003; Dingemanse & Reale 2005) or a ‘behavioural syndrome’ (Sih *et al.* 2004a; Sih & Bell 2008). Individual differences in behaviour are known for many species, ranging from microbes to humans (Gosling & John 1999; Sih *et al.* 2004b; Reale *et al.* 2007) and have been described for a number of different behaviours, such as aggressiveness (Huntingford 1976), exploration (Dingemanse *et al.* 2002), responses to novel stimuli (Mettke-Hofmann *et al.* 2002) and also the level of cooperativeness (Arnold *et al.* 2005; Bergmüller & Taborsky 2007; Charmantier *et al.* 2007; Schürch & Heg 2010a,b).

Consistent individual differences in behaviour pose a number of problems for the existing theory. First, consistency in behaviour is in contrast to the view that behaviour is largely plastic. This is a particular

challenge for social behaviours, which are usually assumed to be adjustable to each situation. Many evolutionary explanations for observed patterns of social behaviour rely on the existence of flexible phenotypes, which are adjusted to the prevailing social landscape, such as the presence and behaviour of competitors, mates or cooperation partners. Why then, do we observe that individuals are consistent in their social behaviour? Second, assuming the existence of an optimal behavioural phenotype, natural selection should reduce genotypic variation over time (Fisher 1930). However, behavioural phenotypes typically show heritable variation, which appears not to be eroded by selection (Penke *et al.* 2007; Reale *et al.* 2007). How is this variation in behavioural phenotypes maintained? Third, behavioural traits are sometimes integrated suites of behaviours, such as the frequently found positive correlation between aggressiveness and boldness (Sih & Bell 2008). Why are behaviours often correlated, sometimes even between apparently functionally independent contexts? Animal personality has been found to be heritable (van Oers *et al.* 2005; Reale *et al.* 2007) and to affect fitness (Dingemanse & Reale 2005; Smith & Blumstein 2008) showing that it is subject to evolutionary change. Hence, we need to

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One contribution of 14 to a Theme Issue ‘Cooperation and deception: from evolution to mechanisms’.

understand how selection can result in the variation we observe and how this variation in turn affects other evolutionary processes.

2. WHY IT IS CRITICAL TO UNDERSTAND THE CAUSES AND CONSEQUENCES OF COOPERATIVE PERSONALITY

Research over more than 40 years has clarified that cooperative behaviour can be understood by considering the phenotypic and genotypic context in which behaviour is expressed (Hamilton 1964; Lehmann & Keller 2006). Inclusive fitness theory predicts that individuals will only invest by helping others when they either receive indirect benefits (by helping relatives) or direct benefits from the receiver (Trivers 1971; Connor 1986) or third parties (Alexander 1987; Wedekind & Milinski 2000). Thus, cooperative behaviour should be favoured by selection when there is a non-random association between phenotypes or genotypes of social partners. This often assumes some degree of conditionality, so that cooperative behaviour is targeted towards kin or individuals likely to express beneficial behaviours. This implies that individuals can adjust whether and how much they will help others. However, as we will outline in this paper, consistent individual variation in cooperative behaviour is apparently widespread in animals.

Although a number of studies have investigated individual variation in behaviour (Reale *et al.* 2007; Sih & Bell 2008), few were specifically designed to study individual variation in cooperativeness. Hence, cooperative personalities or individual differences in cooperative type have been almost entirely neglected in research on the evolution and stability of cooperation (Axelrod 1984; Trivers 1985; Alexander 1987; Dugatkin 1997; Hammerstein 2003; Henrich 2004; van Schaik & Kappeler 2006; Henrich & Henrich 2007), though such inter-individual variation may play a central role for the evolution and stability of cooperation (Komdeur 2006, 2007; McNamara & Leimar 2010).

Given the sparseness of data and theory that addresses individual variation in cooperativeness, we aim at giving a broad overview of the issue, using the term cooperation in a broad sense and also considering the antagonists of cooperation, such as conflict and competition and the antagonists of cooperative behaviour, such as defecting and cheating. A fine-scaled terminology for the study of helping that distinguishes between behaviours and interactions on the one hand and between immediate and lifetime fitness consequences of behaviours or interactions on the other hand has recently been provided (Bergmüller *et al.* 2007; Bshary & Bergmüller 2008). Here, we generally use this terminology, but will often also use terms that are related to cooperative personality (e.g. sociability, agreeableness, division of labour, affiliative behaviour) or non-cooperative personality (e.g. exploitation, hyper-aggression, psychopathy), which are not commonly used in the field but have been used in the studies we describe. Also, we do not explicitly explore the causes and consequences of cooperative personality according to this fine-scaled distinction, as this may be the subject of further study and analyses.

Here we use the term helping (or cooperating) as any action that increases the fitness of the receiver, including apparently altruistic behaviours (behaviours that increase the fitness of relatives thereby promoting the actors' own genes; Hamilton 1964; West *et al.* 2007), cooperative investments in others that lead to a return on investment by the receiver or third parties (Bergmüller *et al.* 2007; Bshary & Bergmüller 2008), including behaviours that serve for conflict resolution (Aureli & de Waal 2000), and self-serving behaviours that result in by-product benefits for others (e.g. selfish herd effects; Hamilton 1971; Connor 1995). In contrast, behaviours that decrease the fitness of others and may destabilize cooperative interactions and relationships include aggressive behaviours, cheating, defection, predation and social parasitism. These behaviours often result in interactions that decrease the fitness of all involved parties, i.e. in conflict and competition (for another view, see Jensen 2010).

The aims of this paper are to provide an overview of the prevalence of cooperative personality in different taxa (§3), to describe evolutionary routes to consistency, individual variation in cooperative types and correlations among behaviours (§4), to explore the evolutionary consequences for the stability of cooperation resulting from personality (§5), to outline promising routes to study cooperative personality (§6) and to highlight some key open issues that need further study (§7).

3. EMPIRICAL EVIDENCE FOR INDIVIDUAL DIFFERENCES IN COOPERATIVE BEHAVIOUR

Individual variation in the propensity to cooperate has been described in a wide range of taxa (table 1). These studies also include a wide range of cooperative phenomena, such as reproductive allocation and restraint, helping in cooperatively breeding species, cooperative foraging, predator inspection and behaviour in economic games. Many of these studies did not explicitly investigate intrinsic individual differences in cooperativeness, so alternative explanations, such as variation in current condition or social or physiological state, may contribute to the reported variation. Future studies will be needed to disentangle the extent to which variation is intrinsic (i.e. animal personality) or state-dependent (i.e. phenotypically plastic) or an interaction of both (Dingemanse *et al.* 2010). The examples show that individual variation in the propensity to cooperate can either be qualitative (i.e. individuals can either vary in whether or not they cooperate or in the type of cooperative behaviour they perform), or quantitative (i.e. individuals vary in the amount of cooperative behaviour they display).

4. EVOLUTION OF COOPERATIVE PERSONALITY

There are three fundamental questions that must be addressed to understand the evolution of individual variation in behavioural type: (i) Why are individuals consistent in the level of cooperative behaviour? (ii) Why do individuals differ in cooperative type? and (iii) Why is cooperative behaviour correlated with other behaviours?

Table 1. Empirical examples for individual differences in cooperative behaviour across different taxa.

species	context	individual differences	references
invertebrates			
<i>microbes</i>			
soil-living social amoebae (<i>Dictyostelium discoideum</i>)	formation of stalk and fruiting body	'cheating' clones selfishly promote their own reproduction at the cost of the 'altruistic' clones	Fortunato <i>et al.</i> (2003)
<i>Cnidaria</i>			
social anemone (<i>Anthopleurea elegantissima</i>)	clonal aggregations of social anemones	small polyps forgo reproduction and defend against other clones, large polyps at the centre produce gonads	Ayre & Grosberg (2005)
<i>insects</i>			
honeybee (<i>Apis mellifera</i>)	reproduction	royal subfamilies within worker populations give rise to new queens	Chaline <i>et al.</i> (2003) and Moritz <i>et al.</i> (2005)
cape bee (<i>Apis mellifera capensis</i>)	reproduction and foraging	some worker subpopulations are less effective foragers, instead they develop ovaries and attain queen-like status within colonies	Moritz & Hillesheim (1985) and Hillesheim <i>et al.</i> (1989)
leaf-cutting ant (<i>Acromyrmex echinator</i>)	reproduction	rare patrilineal cheat nest mates by developing into queens instead of workers	Hughes & Boomsma (2008)
paper wasp (<i>Polistes dominulus</i>)	nest founding	some wasps adopt cooperative strategy (nest founding), while others are more selfish (nest adopting)	Starks (2001)
vertebrates			
<i>fish</i>			
cichlid (<i>Neolamprologus pulcher</i>)	helping	individual differences in amount and type of help provided	Bergmüller & Taborsky (2007) and Schürch & Heg (2010a,b)
three-spined stickleback (<i>Gasterosteus aculeatus</i>)	predator inspection	individual differences between bold and cautious individuals	Milinski (1987)
guppy (<i>Poecilia reticulata</i>)	predator inspection	population and individual differences	Bleakley <i>et al.</i> (2006)
<i>reptiles</i>			
common lizard (<i>Lacerta vivipara</i>)	dispersal, sociality	variation in sociability associated with dispersal patterns	Cote & Clobert (2007)
<i>birds</i>			
noisy miner (<i>Manorina melanoccephala</i>)	helping	provisioning and predator defence are negatively correlated	Arnold <i>et al.</i> (2005)
Seychelles warbler (<i>Acrocephalus sechellensis</i>)	helping at the nest	individual differences in the propensity to help or budding-off of separate territories	Komdeur & Edelaar (2001a,b)
western bluebird (<i>Sialia mexicana</i>)	helping at the nest	heritable variation in the propensity to help or breed independently	Charmantier <i>et al.</i> (2007)
house sparrow (<i>Passer domesticus</i>)	foraging	parental role models determine whether individuals become producers or scroungers	Katsnelson <i>et al.</i> (2008)
<i>mammals</i>			
lion (<i>Panthera leo</i>)	reaction to territory intrusion	some individuals rapidly approach intruders, others lag behind	Heinsohn & Packer (1995)
	task-sharing in cooperative hunting	some individuals circle prey, others wait in the centre for the prey	Stander (1992)
bottlenose dolphin (<i>Tursiops truncatus</i>)	hunting	consistent roles in cooperative hunting	Gazda <i>et al.</i> (2005)
marmot (<i>Marmota flaviventris</i>)	greeting and allo-grooming	cooperative tendencies related to life-history traits and risk-associated behaviour	Armitage (1986)
naked mole rat (<i>Heterocephalus glaber</i>)	helping	some individuals specialised to dispersing instead of helping	O'Riain <i>et al.</i> (1996)
chimpanzee (<i>Pan troglodytes</i>)	hunting	consistent roles in cooperative hunting	Boesch (2002)
rhesus macaque (<i>Macaca mulatta</i>)	social interactions	agreeableness predicts affiliative interactions	Capitanio (1999)

(Continued.)

Table 1. (*Continued.*)

species	context	individual differences	references
vervet monkey (<i>Chlorocebus pygerythrus</i>)	social interactions	calmness scores of infants predict number of social relationships later individual differences in social competence, in part related to rank	Weinstein & Capitanio (2008) McGuire <i>et al.</i> (1994)
humans (<i>Homo sapiens</i>)	experimental economic games	individual differences in the propensity to cooperate	Ostrom <i>et al.</i> (1999), Kurzban & Houser (2001) and Milinski <i>et al.</i> (2008)
humans (<i>Homo sapiens</i>)	experimental economic games	heritable variation in the propensity to cooperate	Wallace <i>et al.</i> (2007) and Cesarini <i>et al.</i> (2008)

(a) *Why is there consistency in the level or type of cooperative behaviour?*

We present three main classes of explanations for consistency in cooperative behaviour. First, individuals may gain fitness benefits from being consistent. Second, differential expression of behaviour in different contexts may be limited or costly. Third, consistency in behaviour may arise because of a dynamic feedback between the strategic decisions of individuals and their physiological or social state, so that the behavioural decisions of individuals are self-reinforcing and reflect the developmental and social history of the individual.

(i) *Benefits of consistency*

Group level return benefits from task sharing

If groups compete with each other, and those with higher specialization among their members out-compete groups with less specialized individuals, group level feedback may favour specialization among individuals if groups are either composed of close relatives or group members are otherwise highly interdependent (Roberts 2005). A number of studies have shown some degree of specialization and task sharing with regards to cooperative tasks in animals, for instance in eusocial insects (Johnson 2005), shoaling fish (Dyer *et al.* 2008), cooperatively breeding vertebrates (Arnold *et al.* 2005; Bergmüller & Taborsky 2007) and cooperative hunting species, such as lions (Stander 1992; Heinsohn & Packer 1995), dolphins (Gazda *et al.* 2005) and chimpanzees (Boesch 2002). Task sharing has recently been found to increase reproductive output in a cooperatively breeding bird (Ridley & Raihani 2008). If task-sharing benefits make groups more efficient (Holbrook *et al.* 2009), this should select for behavioural consistency. Moreover, the degree of specialization should be positively correlated with relatedness among group members or other factors contributing to within-group interdependence among groups.

Benefits of specialization

Benefits of consistency can arise when specialists are more efficient than generalists. For instance, in ants with morphological castes, certain types of individuals have been found to be more efficient in performing

certain tasks than others (Beshers & Fewell 2001). Specialization is also thought to increase efficiency in species without morphological specializations and many studies simply assume that if there is specialization, this corresponds to improved performance in the respective task, which is not always the case (Dornhaus 2008). Hence, even if generalists incur increased costs when compared with specialists, a combination of specialists and generalists may often prevail (D'Orazio & Waite 2008).

Commitment

Consistency may be of benefit to individuals if it changes the expected strategic decisions of social partners in ways that benefit the consistent individual. In game-theoretical terminology, such a sacrifice of behavioural options is referred to as a *commitment* (Schelling 1960). Several theoretical models suggest commitment as a plausible explanation for consistency in cooperative behaviour (McNamara & Houston 2002; Hamilton 2004; Dall *et al.* 2005). For example, commitment can be maintained by means of a credible promise to refrain from reproduction (through the loss of reproductive ability), if the ability to detect violation of such promises is high (Hamilton 2004).

Promises and threats can only influence the outcome of strategic interactions if they can be credibly communicated to social partners. One intriguing possibility is that, when individuals eavesdrop on the behaviour of others, consistency may provide information on the credibility of potential social partners (see also Earley 2010). There is some evidence that cooperative behaviour may have value as a signal (Doutrelant & Covas 2007). Evidence for the role of reliability in generating individual differences in cooperative behaviour comes from a model of the trust game with role asymmetries, in which one player chooses whether to interact and the other, whether to cooperate (McNamara *et al.* 2009). Player one can acquire limited information about the behaviour of other players and assess their trustworthiness before making its move. This model predicts consistent variation between individuals in trustworthiness.

The origins of commitment are problematic at first glance, because the acquired benefits entirely result from the responses of partners. Therefore, we expect

commitment to evolve when social partners are able to directly assess costliness and respond in self-serving ways. For example, if punishment of subordinates is directly related to the actual threat they pose as reproductive competitors, then a subordinate strategy of limiting that threat to reduce punishment could evolve (Hamilton 2004). In Hamilton's model, consistency reduced the information acquisition costs for other group members, so that trust of credibly committed individuals was also favoured.

Reduced conflict owing to social consistency

Individuals may benefit from consistency in behaviours by reducing conflict with conspecifics. Such specialization is known from intraspecific food competition. For instance, individual feral pigeons (*Columba livia*) show greater diet specialization when competition for food is high (Giraldeau & Lefebvre 1985; Inman *et al.* 1987). Individual differences among conspecifics in resource use has been documented in a wide range of species (Bolnick *et al.* 2003). Consistency in behaviour may be a means to reduce conflict among group members because non-overlapping social niches reduce the level of conflict compared to when individuals use all available social strategies (Bergmüller & Taborsky in press).

(ii) *Consistency owing to costs and limits to flexibility*

There are various costs and limits in contributing to low phenotypic plasticity (DeWitt *et al.* 1998) and flexibility of cooperative behaviour may be influenced by many of these. Consistency in behaviour may result from genetic, physiological or developmental limits, costs of flexibility, or because the information necessary for expressing conditional behaviour is costly or unavailable. If information acquisition is costly, then a consistent behavioural type may be favoured over conditional behaviour (McElreath & Strimling 2006). We also draw attention to the potential importance of limitations imposed by the expression of cooperative traits in the context of other traits (epiphenotype). Consistency and variation in cooperative behaviour may result if it can only be expressed in the context of another trait; for example, if it depends on dispersal behaviour (e.g. only non-dispersing individuals can be cooperative), then dispersal strategy could limit the set of possible cooperative behaviours.

(iii) *Consistency through positive feedback*

Positive feedback between state variables such as size, competitive ability or condition and state-dependent behavioural decisions has been hypothesized to contribute to behavioural correlation over time (Dall *et al.* 2004; Sih & Bell 2008). According to this hypothesis, individuals become locked into different regions of state space because of environmental or social feedback, and therefore exhibit consistent behavioural tendencies that differ depending on state. For instance, suppose that individuals in high body condition are more cooperative than those in poor condition, because they can better afford the expenditure. If cooperative individuals gain from the synergistic effects of cooperation, this would then feed back by

maintaining their high body condition. Such self-consistent behaviour could also arise through learning or other developmental processes, where differences in experience may result in subtle and sometimes pronounced phenotypic differences between individuals (West-Eberhard 2003).

(b) *Why is there individual variation in the propensity to cooperate?*

Our definition of personality includes between-individual variation in behavioural traits, including variation in whether individuals are consistent (Dingemanse *et al.* 2010; Reale & Dingemanse 2010). Several evolutionary processes have been proposed to explain different personality types in a population, including frequency-dependent selection (Dall *et al.* 2004), density-dependent selection (Wilson *et al.* 1994) and spatio-temporal environmental heterogeneity (Dingemanse *et al.* 2004). Additionally, based on the finding that intraspecific conflict and competition can entail disruptive selection and thus may be an important causal agent in the evolution of individual variation (Bolnick 2004), negative frequency-dependent processes resulting from social competition in a multi-niche social environment may lead to individual variation in social roles and associated personality types thereby generating individual differences in behavioural strategies (Bergmüller & Taborsky in press; see also §4c(ii)) including the stable coexistence of cooperative and non-cooperative types.

(c) *Why are there correlations between cooperative and other behaviours?*

Behavioural correlations have been found to prevail among different functional contexts and have been termed 'behavioural syndromes' (Sih *et al.* 2004a). Behavioural correlations can either be a result of common underlying proximate mechanisms (pleiotropic effects) that persist despite their fitness costs or result from correlational selection favouring particular trait combinations. Below, we explore examples for both possibilities with regards to cooperative behaviour.

(i) *Pleiotropic effects and spill over*

Although it is often assumed that selection acts independently on different behaviours, there is evidence that strong selection on behavioural phenotypes in one context may favour phenotypic traits that spill over into other, less appropriate, contexts (Sih & Bell 2008). A potential case of such pleiotropic effects is a phenotypic correlation between behaviours in different contexts in fishing spiders (*Dolomedes fimbriatus*; Arnqvist & Henriksson 1997). Similar effects may also exist in cooperative behaviours. As aggressive behaviour often tends to be positively correlated with boldness (Sih & Bell 2008), we might also expect that cooperative behaviour might be positively correlated with shyness or fearfulness. There is preliminary evidence for such a relationship in cleaner wrasses (*Labroides dimidiatus*). Data from laboratory experiments suggest that more shy individuals (more neophobic towards a novel object) are more likely to

cooperate with clients by refraining from cheating and by providing tactile stimulation in an experimental situation (R. Bergmüller, A. Pinto & R. Bshary 2010, unpublished data). Such correlations may be governed by more general traits such as differences in susceptibility to stress and responsiveness to external stimuli. The potential role of hormones for stabilizing phenotypes is discussed by Soares *et al.* (2010). If cooperative behaviour can serve to reduce or pre-empt punishment (Bergmüller & Taborsky 2005), then shyness and the amount of cooperative behaviour displayed can both be expressions of a common underlying trait (e.g. susceptibility to stress) or a responsive personality (Wolf *et al.* 2008).

Helping in cooperatively breeding species has been hypothesized to result from strong selection for parental care and spill over of such care to other contexts (the 'unselected hypothesis of helping'; Jamieson & Craig 1987; Jamieson 1991). This hypothesis suggests that helping could merely be a secondary consequence of selection for the ability to raise own offspring. While this suggestion resulted in some debate (Emlen *et al.* 1991), it has also clarified that helping behaviour should be regarded as a behaviour that is a mixture of constraints imposed by ontogeny and phylogenetic heritage and an adaptive response to particular selective pressures (Wright 1999).

(ii) *Adaptive behavioural syndromes owing to correlational selection*

Adaptive behavioural correlations can result if multiple ecological or social challenges favour particular trait combinations. This can result in (i) correlational selection or (ii) correlational behavioural trait development (i.e. correlated developmental plasticity resulting from social character displacement combined with permanent environmental effects; Bergmüller & Taborsky *in press*). Correlational selection can favour certain combinations of traits (Lande & Arnold 1983). For instance, correlational selection has been shown to favour certain combinations of colour patterns and escape behaviours in garter snakes (Brodie 1992). Until now, few studies have shown that correlational selection can maintain correlations between personality traits. A study on 1101 Australian postmenopausal women combined the results of a personality survey using the Eysenck Personality Questionnaire with the number of children the women gave birth to throughout their life (Eaves *et al.* 1990). Interestingly, lifetime reproductive success was highest in females that were high extravert and low neurotic, or low extravert and high neurotic. In contrast, women with intermediate score combinations had intermediate fitness and high–high and low–low combinations had lowest fitness values. Neither personality dimension had fitness effects on its own, suggesting that it is indeed the combinations of traits that are subject to selection (Sinervo & Svensson 2002).

Correlated characters may also result from developmental diversification in a multi-niche environment during ontogeny, which may result in alternative life-history trajectories (Bergmüller & Taborsky *in press*). For instance, in helpers in cooperatively

breeding species, subordinates may choose between two life-history options: either stay and help and queue for the breeding position or disperse early in order to breed independently (Kokko & Ekman 2002). Initial differences in explorative tendency may result in correlated behaviours corresponding to a disperser or helper strategy. The results of behavioural tests with subadults in a cooperatively breeding fish are in accordance with this prediction (Bergmüller & Taborsky 2007). Across helpers, there was a positive correlation between exploration behaviour and aggressive helping (territory defence) and a negative correlation between territory defence and territory maintenance. There are at least two adaptive explanations for these correlations: either there is differential selection on particular combinations of traits, or conflict between helpers for social roles results in ontogenetic specialization.

5. HOW DOES PERSONALITY AFFECT THE EVOLUTION AND MAINTENANCE OF COOPERATION?

(a) *Variation in cooperativeness promoting cooperation*

(i) *Cooperation owing to extrinsically caused variation*

Extrinsically induced variation in cooperativeness in a population can lead to feedback mechanisms that further promote the persistence of different behavioural types. Formal models have explored the effects of consistent individual differences in the propensity to cooperate on the stability of cooperation in the Prisoners' Dilemma and other social dilemmas (McNamara *et al.* 2004, 2009). In the Prisoner's Dilemma, the highest payoff for any player is to defect, regardless of the behaviour of its partner. However, mutual defection results in a lower individual and global payoff than mutual cooperation. In the iterated version of the Prisoners' Dilemma, the only Nash equilibrium is mutual defection starting in the first round if the number of rounds is finite and known to the players. McNamara *et al.* (2004) analysed a game where players could play the Prisoners' Dilemma with the same partner for 100 rounds but the interaction would be terminated if one of them cheated. Mechanisms extrinsic to the game were assumed to contribute to variability in strategies. This resulted in variation in the expected duration of interactions with social partners, so that, while the total number of rounds was finite and known, the number of rounds with a particular partner was less predictable. The evolutionary stable strategy (ESS) solution to this game was a distribution of strategies that plays a different number of rounds cooperatively before cheating (McNamara *et al.* 2004). Thus, the contribution of extrinsic factors to variation in game payoffs resulted in both the maintenance of cooperation and the maintenance of variation in strategies in the game.

In public goods games, individuals gain by contributing to a common good but individuals that do not contribute gain most. The theoretical expectation is that non-zero contribution should quickly be eliminated from a population playing such a game (Hardin 1968). In contrast, the addition of a behavioural type that participated optionally (loners) in an

experimental public goods game resulted in the maintenance of substantial levels of cooperation in a rock–paper–scissors dynamic (Hauert *et al.* 2002; Semmann *et al.* 2003). When defectors were most frequent, loners increased in frequency. However, when loners became more common, the frequency of cooperators increased, which in turn were later invaded by defectors.

(ii) *Social reliability, social identity and fine-tuned social signals*

As discussed in §4a(i), personality may stabilize cooperation if consistency in behaviour signals social reliability (i.e. due to commitment). If signalling of consistency is important, this may promote the use of identity traits that promote individual recognition in a social environment (Johnstone 1997; Dale *et al.* 2001; Tibbetts & Dale 2007). Such traits would permit tracking of repeated cooperative interactions and fine-tuning of behavioural interactions. While behaviours often allow for a broad recognition of the motivation of explicitly aggressive or socio-positive behaviours within species, fine-tuned recognition of subtle signals may often only be possible if individuals know each other's personality, i.e. when they know the stable responses of social partners in cooperative and non-cooperative interactions.

(iii) *Stabilizing cooperation by punishment or self-serving harassment*

Punishment can stabilize cooperation (Boyd & Richerson 1992; Clutton-Brock & Parker 1995; Gächter *et al.* 2010; Jensen 2010), particularly if individuals cooperate in order to avoid punishment (Bergmüller *et al.* 2007). However, this creates the problem to explain why individuals perform costly and risky punishment. A second-order dilemma may result because those that fail to punish appropriately still gain the benefits from others' efforts. Personality provides a potential solution. In humans, the neural reward systems are activated if test subjects punish individuals that deviate from social norms (de Quervain *et al.* 2004). Hence, variation in the tendency to feel pleasure when punishing defectors could result in individual variation in the tendency to punish. Moreover, variation in personality dimensions such as extraversion may be involved, as more extravert individuals may be more likely to actually punish. Such factors may also be involved in explaining 'altruistic punishment' (Fehr & Gächter 2002), i.e. individuals punish unfamiliar individuals that deviate from social norms, thereby stabilizing cooperation in humans. While altruistic punishment has been hypothesized to result from relatively complex evolutionary mechanisms, such as cultural group selection (Fehr & Fischbacher 2003), animal personality provides a simpler alternative explanation. If intrinsic or extrinsic mechanisms maintain variation in aggressiveness, and this aggressiveness is more probably directed towards defectors than cooperators (for instance, because it is less costly to direct aggression towards defectors), cooperation can be stabilized as a by-product of self-

serving harassment (i.e. 'pseudo-punishment'; see also Lehmann *et al.* 2007).

(b) *Variation in cooperativeness disrupting cooperation*

(i) *Hyper-aggressive individuals and 'animal sociopaths'*
Evolutionary explanations of cooperative behaviour focus on the problem of how cooperation can prevail despite the prevalence of cheaters. Unconditional cheating can be an ESS (Mealey 1995; Wischniewski *et al.* 2009). If social peace is regarded as a common resource, extremely aggressive or uncooperative individuals can be regarded as cheaters who exploit this resource. For instance, in water striders hyper-aggressive males cause a breakdown of mating activity in the whole population compared with populations without extreme individuals under laboratory conditions (Sih & Watters 2005). In yellow baboons, one hyper-aggressive male immigrant caused various deleterious effects on other group members, such as abortions by three pregnant females following constant harassment and a considerable increase in stress hormone levels in all group members (Alberts *et al.* 1992). In humans, extremely non-cooperative individuals that relentlessly exploit others often fall into the category of 'sociopaths' or 'psychopaths' (Blair 2006; Blair *et al.* 2006; Hare & Neumann 2008). Psychopaths are characterized by a lack of remorse and an inability to feel sympathy for other living creatures. In the extreme, individuals with this emotional 'dysfunction' have been described as 'human predators' that consider other people merely as a source for exploitation. To our knowledge, it has not been investigated whether non-human animal psychopaths exist. We would expect such types particularly in species with 'other regarding preferences' (unsolicited prosociality: individuals spontaneously help non-reciprocating and unrelated individuals, which is interpreted as a concern for the welfare of others). Positive selection for 'other regarding preferences' has been proposed for species with highly interdependent social interactions such as cooperatively breeding species (Burkart *et al.* 2007; Burkart & van Schaik 2009; Jaeggi *et al.* 2010). In such species psychopathic types could exploit the social predispositions of others. Highly uncooperative individuals should be an important focus of research when aiming to understand the level of cooperation prevailing in a population as they can be 'keystone individuals' (Sih & Watters 2005; Flack *et al.* 2006) because of their disproportionate effect on the social climate (Alberts *et al.* 1992; Beehner *et al.* 2005).

(c) *Additional factors that may influence the effects of variation on cooperative personality*

(i) *Social networks and social hierarchies*

In real-world situations, organisms rarely interact randomly, but tend to interact with certain individuals more often than with others (Krause *et al.* 2009; Sih *et al.* 2009). This variation in the frequency of interactions with certain individuals of a population can be studied with network analyses (Krause & Ruxton 2002; Croft *et al.* 2009). This allows for investigating

the effects of particular features of the network, such as the type of network, the number of interaction partners or the relative position of certain individuals in a network. Social network parameters can influence the effects of cooperative or uncooperative actions on the population level of cooperation. For instance, cooperation can spread if the average number of neighbours in the network is lower than the benefit to cost ratio of a cooperative act (Ohtsuki *et al.* 2006). Individual variation in behavioural phenotype may also determine network structure (Pike *et al.* 2008; Weinstein & Capitanio 2008).

Different social network structures may also provide opportunities for different social roles within and between groups. For instance, bottlenose dolphins (*Tursiops* spp.) have brokers that facilitate interactions between different groups (Lusseau & Newman 2004). Future issues include understanding how certain individuals obtain particular network positions and how this affects the cooperative climate within the group through feedback mechanisms such as generalized reciprocity (Rutte & Taborsky 2007). The interaction between network structure and the influence of individuals on group-level properties is another emerging topic. For example, after the death of aggressive males, the social climate of a baboon group changed and became more affiliative and less stressful (Sapolsky & Share 2004). Such personality effects on group phenotypes should be particularly important with respect to well-connected or high-status individuals.

(ii) *Spill over: synergistic effects*

In principle, spill over of behaviour across contexts could allow cooperative behaviour to invade uncooperative populations. Asymmetrical costs of mistakes may result in the effect that misdirected help is consistent: for example, if it is less costly to care for non-relatives than to not care for relatives, cooperative behaviour among non-relatives might be maintained at some frequency. In some games, cooperative behaviour among non-relatives has a high invasion threshold; that is, a fairly large proportion of the population must already be cooperative before selection favours cooperation. Spill over from strong selection for cooperative behaviour in other contexts, such as cooperation with relatives, may provide such initial conditions.

6. HOW TO STUDY PERSONALITY IN THE CONTEXT OF COOPERATION

(a) *Modelling the evolution of cooperative personality*

One approach to modelling the evolution of suites of correlated social behaviours is to use a partitioned version of Price's equation (Price 1970) to model how within- and between-individual genotypic and phenotypic covariance influence selection on a set of traits of interest. This could include a suite of different, but correlated behaviours, or a qualitatively similar behaviour expressed in different contexts. The strength of phenotypic selection on multivariate social traits

has been derived as follows (Wolf *et al.* 1999a):

$$s = P\beta_n + C^I\beta_s$$

In the above equation, P is the within-individual phenotypic variance–covariance matrix or, in other words, a matrix describing the structure of phenotypic behavioural syndromes in a population. C^I is the between-individual phenotypic covariance matrix. Non-zero elements in this matrix mean that interactions among individuals are non-random with respect to phenotype. β_n is the vector of phenotypic selection gradients on the actor's fitness and β_s is the vector of phenotypic selection gradients resulting from the traits of social partners. The vector of strengths of phenotypic selection on the traits of interest is s . In principle, P and C^I are measurable, although in practice there are many challenges inherent in measuring behavioural syndromes in social settings, as discussed elsewhere in this review. Evolutionary biologists are often more interested in the effects of selection on trait evolution over long time scales, which introduces two problems. The first is that the above formulation models the strength of phenotypic selection, but not trait evolution *per se*. This is not an insurmountable problem, but it requires careful decomposition of the phenotypic covariance matrices into additive genetic, environmental and indirect genetic components. Such an approach has been used to model the evolution of correlated social traits with maternal effects (Cheverud 1984), reciprocal indirect genetic effects (Moore *et al.* 1997) and sexually selected traits (Wolf *et al.* 1999b). Parameterization of these models is substantially more difficult than for strictly phenotypic formulations, because quantification of additive and indirect genetic effects for multiple, interacting traits may present challenges.

The second problem is that the above approach assumes that the P matrix and the C^I matrix are stable. However, both of these matrices are likely to evolve over time. Evolution of the genotypic variance–covariance structure, which underlies the phenotypic variance–covariance matrix, has been extensively explored by quantitative geneticists (Lande & Arnold 1983). The structure of the between-individual phenotypic covariance is influenced by the behavioural decisions of interacting individuals, decisions which themselves include heritable components. Evolutionary game theory (Maynard Smith 1982) and adaptive dynamics approaches (Diekmann 2004) can help inform how social phenotypes that influence the pattern of interactions among individuals, the C^I matrix, evolve.

Adaptive dynamics approaches also provide a promising modelling framework under which to explore the origin of polymorphic phenotypes, such as distinct behavioural syndromes (Leimar 2005). Briefly, adaptive dynamics models investigate whether rare mutations of small effect can invade a resident population. Adaptive dynamics models can incorporate eco-evolutionary feedbacks; the resident strategy may influence population size, resource availability and the social landscape, all of which may feed back on the selective landscape for the trait in question. Several of the explanations for behavioural syndromes

discussed in this review involve such social or ecological feedbacks, so that behavioural decisions are self-reinforcing. A second, and related, key benefit of adaptive dynamics models is that they often predict evolutionary branching. As the fitness landscape for (possibly multiple) invading phenotypes changes in response to changes in the resident phenotype, the population may experience disruptive selection. Biologically, evolutionary branching has been used to explain the emergence of genetically determined polymorphic phenotypes, including cooperative polymorphisms (Doebeli *et al.* 2004).

Adaptive dynamics models have been used to explore whether selection will result in the evolution of distinct cooperative types. In a spatially explicit model of the coevolution of mobility and altruism, there was no evolutionary branching (Le Galliard *et al.* 2003). In the continuous Snowdrift game, evolutionary branching and coexistence of high- and low-cooperative phenotypes have been found when costs and benefits of cooperation are saturating (Doebeli *et al.* 2004), which may be relevant when the costs of initiating cooperative investment are much greater than the cost of continuing such investment.

(b) Empirically

A considerable challenge of studying cooperative or other social personality traits is to disentangle individual variation from variation arising through social interactions and non-social factors. In group-living species, social effects such as position in a social hierarchy, group size, demography or sex ratio may influence behaviour, but might also covary with the personalities of group members. Hence, decomposition of variance into individual effects, interactions between individuals and group-level effects quickly becomes a difficult task. Below, we propose potential solutions to deal with this problem.

(i) Individual variation in the propensity to cooperate and social consequences

Personality traits traditionally are measured using standardized tests such as exploration tests, aggression tests or tests for neophobia (Wechsler 1995; Gosling 2001; Bell 2007; Reale *et al.* 2007). There is a need for similar standardized tests for cooperative behaviour. For some systems, such as cooperatively breeding fish, standardized measures of cooperative behaviour have been developed (Bergmüller & Taborsky 2007; Schürch & Heg 2010a). For any personality tests, repeated behavioural measurements are necessary to determine whether individuals differ from one another consistently. This permits estimation of the repeatability of relative behavioural response scores (Lessells & Boag 1987; Bell *et al.* 2009). Behavioural scores obtained under standardized tests can be used to analyse whether they have consequences on social interactions under realistic conditions (Dingemanse & Reale 2005).

By design, standardized tests remove variation in the social context, so it is necessary to compare the results of these tests with behaviours measured under more natural social conditions. However, cooperative

behaviour under such conditions depends not only on the focal individual's cooperativeness and group-level effects such as group size, but also on the behaviour and the personality of social partners. A promising approach to exploring the structure of social-behavioural variation is to measure interactions among all social partners (Malloy *et al.* 2005), and partition variation into actor effects, partner effects and emergent relationship effects (Gosling 2008). This approach necessarily is very data intensive and may not be possible for some cooperative interactions.

A useful technique to obtain data on individual differences in social situations may be observer ratings in which observers intuitively rate the behaviour of subjects according to pre-defined classes. A recent comparison of observer ratings with behaviour coding techniques suggests that reliability of observer ratings is high and both can in some cases yield comparable results (Vazire *et al.* 2007). Provided that behavioural classes are carefully defined to minimize anthropomorphism, behavioural ratings may be helpful to better understand the prevalence and the consequences of personality variation in realistic social settings (Vazire *et al.* 2007).

(ii) Behavioural correlations

Much of the research about behavioural correlations is still in the descriptive stage investigating the prevalence of correlated behavioural traits. Ideally, future research will emphasize tests of specific, theory-driven predictions about which behaviours should be related to each other (Sih & Bell 2008). For example, recent studies have tested specific predictions based on life-history trade-offs in cooperatively breeding fish (Bergmüller & Taborsky 2007; Schürch & Heg 2010a). As increasingly large behavioural datasets accumulate across species and behavioural traits, it will be possible to use comparative methods to investigate apparently common patterns across taxa (such as the frequently observed positive correlation between boldness and aggression) and to relate these to historical and ecological factors.

7. CONCLUSIONS AND FUTURE DIRECTIONS

We have shown that individual variation in cooperativeness has been observed in different taxa and we investigated the evolutionary causes of this variation and their consequences for the evolution and maintenance of cooperation. Much of the current research on cooperation is based on the assumption that the expression of cooperative behaviour is conditional upon the behaviours of others. Hence, a key conclusion from our survey is that the existence of individual variation in the tendency to cooperate provides an opportunity for novel developments in the fields of evolutionary and game-theoretic analyses of cooperation. Pure cost-benefit analyses of behavioural interactions that only focus on current payoffs are insufficient if individual differences in the tendency to cooperate exist. Hence, the existence of personality differences urges us to better understand the causes and consequences of personality in social interactions.

Increasing evidence suggests that individual animals differ in both the average level of behaviour displayed across a range of contexts (animal personality) and the responsiveness to social or environmental variation (plasticity). Both aspects show heritable variation and have fitness consequences. The concepts to explain animal personality and behavioural plasticity have recently been unified within a single framework, which is based on the concept of behavioural reaction norms using a quantitative genetics approach to behavioural plasticity (Dingemanse *et al.* 2010). The authors highlight that personality and individual plasticity may also be linked. While much of the cooperation research has focused on the question whether cooperative behaviour will evolve at all, the question of how much each individual will help has received far less attention to date. It will be a future challenge to increase our understanding about the effects of individual changes in the tendency to cooperate depending on environmental and social changes.

An important issue in evolutionary research is the co-development of theory and empirical research. Currently, many of the evolutionary explanations for the existence of animal personality and behavioural syndromes and their influence on the evolution of behaviour are based on verbal models. In order to foster the development of formal analyses, we have provided a general approach to help integrating empirical measurement of covarying behaviours with current quantitative genetic, game-theoretical and adaptive dynamics models. Such models will allow testing of the plausibility of these arguments, as well as generating quantitative and qualitative predictions about how ecological and social variables interact with behavioural syndromes to produce observed behaviours. Future research should further attempt to develop models that allow for empirical testing based on realistic assumptions that have been derived from empirical data.

Animal personality research has the potential to integrate various research areas that are currently developing largely independent from each other. For instance, research on animal personality links evolutionary and ecological questions of why animals behave the way they do tightly to developmental questions and proximate aspects underlying behaviour. Therefore, asking whether individuals differ in behaviour (or suites of behaviours) fundamentally integrates proximate and ultimate aspects of behaviour that are commonly studied more independently from each other (Sih *et al.* 2004a; Bell 2007). Moreover, research on cooperative personality provides an integrative view to animal behaviour that accounts for the 'package nature' of many behaviours. We believe that the study of cooperation will greatly benefit from such an integrative approach.

In conclusion, our review and analyses shows that it will be valuable and necessary to incorporate the causes and consequences of individual variation in behavioural traits in future studies on cooperation. This will allow for a better understanding of the questions why, how and how much individuals cooperate and may provide a linking bridge between research on cooperation in humans and other animals.

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