Animal personality as a cause and consequence of contest behaviour

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Summary

We review the evidence for a link between consistent among-individual variation in behaviour (animal personality) and the ability to win contests over limited resources. Explorative and bold behaviours often co-vary with contest behaviour and outcome, although there is evidence that the structure of these 'behavioural syndromes' can change across situations. Aggression itself is typically repeatable, but also subject to high within-individual variation as a consequence of plastic responses to previous fight outcomes and opponent traits. Common proximate mechanisms (gene expression, endocrine control and metabolic rates) may underpin variation in both contest behaviour and general personality traits. Given the theoretical links between the evolution of fighting and of personality, we suggest that longitudinal studies of contest behaviour, combining behavioural and physiological data, would be a useful context for the study of animal personalities.

Personality, Repeatability, Contest, Aggression, Fight

Introduction

Consistent among individual variation in behaviour, or animal personality [1] is present in a wide variety of taxa [2]. Perhaps most notably, individuals show consistent variation in how they deal with information about risk. When presented with a startling stimulus or a novel object, individuals may differ consistently in their responses over repeated observations. This variation represents a continuum from bold, risk-prone, individuals to shy, risk-averse, individuals. Animal personalities occur in many *contexts* (see ESM for a glossary of key terms) including foraging and exploration [3], provisioning of young [4], vigilance [5] and courtship [6]. When suites of behaviours are correlated across contexts at the among-individual level these are described as *behavioural syndromes* [7]. While among individual variation in biology is not unexpected [8] the presence of animal personalities represents, to some extent, an evolutionary puzzle. In theory, animals have the potential to adjust their behaviour to match the current set of conditions (the *situation*; see ESM). This behavioural plasticity is widely viewed as different from developmental plasticity because behavioural responses can be very rapid and highly reversible. Given that behaviour is highly labile, it can seem surprising that individuals vary consistently in their behaviour at all, rather than converging on a single plastic phenotype that allows expression of the optimal response for any given situation. Indeed, although adaptive behavioural plasticity is often seen, for example in the form of increased mean hiding times in response to heightened predation threat [9], consistent behavioural differences are nonetheless preserved across situations.

Various explanations for the presence of animal personalities have been proposed. For example, behavioural plasticity requires information gathering and assessment activities and therefore may be constrained by the ability to capture and process information [1,10]. Alternatively, the outward expression of behavioural tendencies might reflect underlying variation in metabolic rate [11]. In both scenarios the mechanistic explanation may be

underpinned by life-history trade-offs. First, it is assumed that information gathering is costly such that investment in behavioural plasticity will be to the detriment of other traits and activities. Second, there is an expected trade-off between metabolic rate and longevity, recently formalised as the pace of life syndrome hypothesis [11]. While these hypotheses are grounded in life-history theory, they do not directly explain why the outcomes of trade-offs should vary among individuals. One possibility is cross-generational bet-hedging where parents produce a range of offspring with different phenotypes in the expectation that some will survive [12]. More generally, evolutionary game theory, which models interactions between individuals, can explain the maintenance of animal personality through negative frequency dependent selection. This can lead to the maintenance of variation in contexts ranging from alternate mating tactics to fighting strategies. Indeed, this is the principle of the hawk-dove game, first developed to understand the evolution of animal *contests*, and subsequently used to model the evolution of animal personalities [12].

Despite the link between personality and animal contests made apparent by game theory, this possibility remains relatively understudied by empiricists (Table 1). Nevertheless, animal contest research often focuses on questions of direct relevance to the mechanisms thought to underpin personality variation. First, contests, interactions that involve the use of *agonistic* behaviour, are heavily reliant on information gathering and decision making [13]. Second, contests are energetically demanding, require elevated metabolic rates and lead to post-contest changes in behaviour [14]. Third, individuals usually engage in multiple contests over their lifetime and in each case the situation will be different due to variation in opponent phenotype. Below we review the evidence for links between animal personality and contests, and consider whether they might be underpinned by common proximate mechanisms. Figure 1 summarises these associations.

Agonistic behaviour in behavioural syndromes

Animal contests rarely result in serious injuries, the most common means of contest resolution being through decision-making. The eventual winner is the individual that persists for the greater amount of time while losers terminate contests by deciding to quit. Since these decisions are based on information (about the resource, or relative or absolute fighting ability [14]) we might expect agonistic behaviour to co-vary with behaviours related to information gathering. In the mangrove rivulus, *Kryptolebias marmoratus*, for example, *aggressive* individuals are also the boldest and most explorative [15]. In contrast, in the house cricket *Acheta domesticus*, there are significant correlations between boldness, exploration, anti-predator behaviour and courtship but aggressiveness does not correlate with any other behavioural context [6].

The temporal stability of links between agonistic and other behaviours was studied in hermit crabs, *Pagurus bernhardus*, which take on asymmetric attacking and defending roles during contests over gastropod shells [16]. When startled, hermit crabs withdraw into their shell and the latency to re-emergence provides an assay of boldness, which is repeatable across situations of differing predation risk [9,16]. In contrast, shell investigation behaviour and latency to attack are not repeatable between risk levels, providing some evidence for an individual by environment interaction effect ('IxE') [17]. Crabs that were slow to re-emerge from their shells also showed low investigation and low aggression but this correlation was only seen under low predation risk. Surprisingly, there was no significant correlation in either situation between shell investigation and latency to attack.

Contests involve a range of agonistic behaviours including signals and defensive acts as well as aggression, all of which influence the chance of victory. Thus, in great tits, *Parus major*, while slow explorers were less aggressive than fast explorers they showed more

agonistic behaviour in total [18]. Moreover, in addition to syndromes involving behaviours used in different contexts, the different components of agonistic behaviour may also be correlated at the among-individual level. In laboratory mice, *Mus musculus*, individuals of a SAL (short attack latency) strain show indiscriminate aggression towards standardised opponents, while other strains show a broader mix of agonistic behaviours [19]. Similarly, within fallow deer (*Dama dama*) herds, individuals vary in the consistency (*intra-individual variation*, IIV) of their agonistic behaviour [20].

These studies show that agonistic behaviour and other personality traits can co-vary within syndromes and that among-individual variation is likely to have genetic underpinnings. It is also clear, however, that syndrome structures themselves can be variable and can change across situations.

Is personality a Resource Holding Potential trait?

Regardless of how agonistic behaviour co-varies with other behaviours, the ultimate driver of fitness for a contestant will be whether or not it wins the fight [14]. Therefore, contests could explain consistent variation in traits that correlate with fighting ability, or 'resource holding potential' (RHP). Although aggressiveness can contribute to RHP, the two are not necessarily equivalent. Intuitively, high boldness or a willingness to take risks might help animals to win fights. Bold individuals that spend less time hiding or retreating could have more opportunities for offensive behaviours, make decisions more rapidly or take greater risks in pursuit of victory. Alternatively, shyer individuals might have a defensive advantage. In hermit crabs long startle response durations assessed prior to fighting were associated with a greater chance of winning for defenders but not attackers [21]. In these contests with a clear role asymmetry, personality is potentially an RHP trait for one role but not the other.

In many contests role asymmetries are absent, or at least minimal. In the sea anemone, *Actinia equina*, symmetric contests take place over space. In escalated encounters specialised stinging tentacles are used [22]. *A. equina* show repeatable boldness assayed by the duration of tentacle retraction following disturbance [23]. Prefight boldness correlates with the chance of winning but, in contrast to the situation in defending hermit crabs, losers show longer startle responses than winners [23]. Having a short recovery time may mean that more stings can be landed on the opponent, which increases the chance of victory in escalated fights. Similarly, in contests over dominance status in rainbowfish, *Melanotaenia duboulayi* [24], zebra finches, *Taeniopygia guttata* [25] and domestic fowl, *Gallus gallus domesticus* [5] dominant individuals are consistently more proactive when not fighting and more aggressive during fights.

Thus, personality traits such as boldness not only co-vary with aggressiveness but also, in many cases, with RHP itself. However, the direction of this association varies among study systems and, in asymmetric contests, between roles.

Post-fight personality change

Fighting is a demanding activity and consequently it can lead to post-fight changes in state, in some cases due to injuries but more often as a result of the energetic demands of agonistic behaviour [14]. Therefore, any changes in post-fight boldness might derive from metabolic costs such as the depletion of energy reserves [14]. Similarly, changes in post-fight boldness could derive from changes in endocrine state, although work on *P. major* shows that the extent of such changes can be dependent on *pre*-conflict *behavioural type* [26].

Post-contest behaviour is also important in the rainbow trout, *Onchorhyncus mykiss* [27]. Strikingly, for individuals that were classified as bold at the start of the experiment, simply observing the behaviour of a shy demonstrator was enough to reduce their boldness. Thus in *O. mykiss* boldness, although repeatable, is very labile and highly dependent on social environment. Similarly, bold individuals that lost fights subsequently became shyer. The effect of observing a demonstrator of different behavioural type was absent for fish that started out as shy but winning a fight still emboldened them post-contest. In *A. equina*, losers showed decreased boldness 24h after fighting and repeatability was reduced across consecutive observations interrupted by fighting [23]. In contrast *P. bernhardus* defenders that lost their shells became bolder after the fight whereas for those that resisted eviction withdrawal durations increased [21]. Moreover, the repeatability of startle responses after fights was lower for defenders after fighting compared to pre-fight levels regardless of whether they were evicted or not.

Studies have revealed changes in boldness up to a few days after fighting. Such post-fight personality changes could derive from the 'winner and loser effects' that often follow contests [28]. First, the experience of losing a contest might automatically lead to a reduction in RHP through injuries or loss of resource. In this case the individual might adjust its behaviour to cope with reduced expectations of victory. Alternatively, post-fight changes in boldness could actually contribute to winner and loser effects, via a process of positive feedback and resultant canalisation of behaviour. If losing a contest leads to a consistent change in behaviour and this change equates to a reduction in RHP then the defeated individual will be more likely to lose subsequent contests and, in turn, experience more loss of RHP.

In general, personality traits appear to change following a fight. Typically, losing a fight is associated with reduced RHP, but in asymmetric contests the effects of fighting on subsequent behaviour might be role- as well as outcome-specific.

Repeatability of agonistic behaviour

If winning and losing contests can change post-fight expression of otherwise repeatable behaviours, what about the repeatability of agonistic behaviour itself? This is an especially challenging question to address. In general, aggressive behaviours are moderately repeatable [29]. However, while repeatability of aggression has now been widely estimated in captive and natural populations (recent examples [30–32]), extrapolating estimates derived from standardised behavioural assays (e.g. model opponents) may not be entirely appropriate. This is because in real contests the opponent is a key determinant of the focal individual's behavioural decisions, including whether to initiate a fight, to escalate or de-escalate their agonistic behaviour, and ultimately whether to give up and relinquish the contested resource. While opponents may vary in ways that influence focal behaviour, experimental studies commonly seek to minimise this source of variation. Similarly, contesting pairs are often matched for physical RHP traits (e.g. body size), allowing separation of behavioural from morphological effects on contest outcome. However, size matching may give a misleading view of the importance of escalated aggressive behaviours because contests should escalate more when opponents have similar RHP. It may also upwardly bias repeatability estimates because, if focal behaviour is plastic with respect to opponent phenotype, standardizing the latter will remove a source of within-individual variation.

The consistency of agonistic behaviour is therefore best assessed from repeated measures of focal behaviour across an ecologically relevant sample of opponents. Several

recent studies have exploited experimental designs that not only cope with this added source of variation, but use it to gain additional insights. In male-male contests in green swordtails, *Xiphophorus helleri*, focal behaviours are repeatable but can also be dependent on repeatable opponent effects [33]; just as focal individuals behave consistently, opponent individuals can consistently elicit particular behavioural responses. This was also found in the sheepshead swordtail, *X. birchmanni*, where among-individual (focal and opponent) variance and covariance was estimated for a set of agonistic behaviours [34]. Here, 80% of the among-individual variation was explained by a single axis of aggressiveness. For example, focal individuals that consistently display more to opponents also tended to attack more often and more rapidly. Furthermore, when designated as opponents, these fish elicited more defensive behaviours from focal individuals.

Studies rooted in contest theory tend to test hypotheses about sample level plasticity, for example comparing mean agonistic behaviour between treatments of high and low resource value. In contrast, animal personality studies focus on among-individual variation. The experimental and analytical approaches [35,36] used in quantitative genetic studies of contests and social dominance have the potential to characterise both levels of variation simultaneously, provided repeated contests are available. For instance, while repeatable opponent effects were found in green swordtails, these were not as important as contest-specific effects of relative opponent size; while focal individuals differ in personality, on average they all reduce aggression when faced with a larger opponent [33]. In contrast, plasticity of contest behaviour was less apparent in sheepshead swordtails. Personality, but not relative size, predicted contest outcome with more aggressive males consistently winning. This result supports the idea that personality variation can play an important role in generating variance for fitness-related traits [37].

More generally, it is also important to recognise that while behavioural plasticity and individual consistency have antagonistic effects on repeatability they are not mutually exclusive. In fact, as discussed above there can also be among-individual variation in plasticity, (IxE interactions) [17]. Mixed model methods for estimating focal and opponent repeatabilities are readily extended to test for and quantify IxE. This approach was recently applied in a study on blue tits, where females that defended their nestlings more intensively were actually less aggressive when "defending" themselves against a human handler [38].

In the current context of animal contests, studies of IxE might usefully model focal behaviour across the changing situation imposed by variation in opponent phenotype (e.g. using models with random slope effects) [17]. This would allow us to test whether individuals differ not just in their average aggressiveness, but also in the extent to which they moderate their behaviour according to their opponent.

Mechanisms of variation in agonistic behaviour

It seems clear that aggressive behaviours and other behaviours that contribute to RHP can be repeatable. Nevertheless, repeatable RHP traits are still sensitive to fight outcomes, opponent phenotypes and prior social experiences [39]. Understanding the proximate mechanisms of agonistic behaviour could help elucidate why some RHP traits show this plasticity.

Many studies have explored the proximate mechanisms underlying aggression. In vertebrates, the presence of a competitor can trigger the stress response [14]. This typically involves rapid changes in gene expression, endocrine state and finally the innervation of energy reserves necessary for sustained combat [40]. These crucial physiological reactions could underpin differential performance in fights. More generally, exploration and enhanced

risk taking also require energy, while shyer behaviours conserve energy. In rainbow trout *Onchorhynchus mykiss* the expression of transcripts involved in this cascade are correlated with boldness, which in turn predicts winners of competitive interactions (e.g. [41–43]. Invertebrates have a simpler fight or flight response mediated by biogenic amines that have been linked to contest outcomes [44]. In particular octopamine is higher in winners before and after fights in the shore crab, *Carcinus maenas* [45]. In the cricket, *Gryllus bimaculatus,* octopamine is elevated after activity and its role is analogous with vertebrate corticosteroids in mobilising energy reserves [46]. Thus among-individual variation in fight performance is intrinsically linked to metabolism and energy stores and alterations in boldness often result from a change in energetic status. For example, shy rainbow trout that lost body mass during transport were faster to feed in a novel environment than bold fish that did not lose as much weight [47].

It is clear that energetic status influences both personality and RHP in animal contests, an idea contributing to the pace of life hypothesis [11]. Two models have been proposed to understand the influence of resting metabolic rate (RMR) upon boldness: the Performance Model and the Allocation Model [48]. The Performance Model assumes that behaviours linked to high resource acquisition such as increased aggressiveness, exploration and risk taking should positively correlate with RMR. Conversely, the Allocation Model suggests that for individuals maintaining high RMR little energy is available for other tasks leading to a negative correlation with boldness. Theory predicts that individuals with high RMR should conserve energy which supports the Allocation Model [49]. However, empirical studies have provided support for both models indicating that the context is important. High metabolism is seen in bolder spiders, *Larinioides* sp., [47] and in more dominant birds (*Cinclus cinclus*) [50] and fish (e.g. salmonids, [51]). Indeed, irrespective of context high RMR brown trout, *Salmo trutta*, outcompeted low RMR individuals due to increased foraging rates in high RMR fish

whilst low RMR fish conserved energy by reducing foraging and sheltered more [52]. This may explain why these two distinct behavioural phenotypes coexist since both gained weight during these experiments.

Thus, performance in contests is intimately governed by energetic constraints linked to metabolic rate such that bolder animals show higher rates of aggressive behaviours and longer persistence, potentially giving them an advantage in 'war of attrition' [53] type contests. Metabolic differences that underlie RHP and strategic decisions during contests may, therefore, provide an explanation for consistency across confrontations.

Conclusions

Animal personality research is fundamentally about using longitudinal data to understand the hierarchical nature of variation in behaviour; typically we analyse differences within and among individuals, contexts and situations. Theoretical developments in personality research make it increasingly important that we also try to capture the proximate drivers of this variation – genes, physiologies, ontogeny and previous experiences – as well as its outward behavioural expression. The examples reviewed here highlight the strong tradition for doing precisely this in animal contest research [14, 18], meaning that amenable study systems are already in place. Moreover, in studying contests we necessarily extend the study of variation in behaviour upwards, into the social environment of interactions between individuals.

As well as providing new insights, studies of animal contests also raise new questions relevant to understanding the evolution and maintenance of animal personalities: How much among individual variation in aggressiveness is due to genes as opposed to previous experiences? How flexible is the expression of agonistic behaviour (and of behavioural

syndromes involving it) across different social environments? And finally, to what extend do similar mechanisms underpin variation in contest behaviour and personality across different animal species? Powerful experimental designs and analyses, similar to those already used in quantitative genetics, will be required to address these questions since the links between contests and personality may not always be straightforward. For example, otherwise consistent responses to winning and losing may be modulated by opponent behavioural type. Given the demonstrable links between genes and aggressiveness, studies that use individuals of known relatedness would complement previous work based on different selection lines. Overall, links between fight performance and metabolic rate provide evidence that the mechanisms of variation in performance during contests may also underlie consistency in boldness. We therefore suggest that coupling longitudinal data on fighting with longitudinal data on physiology could be instrumental in resolving the questions about animal personalities discussed above.

Acknowledgements

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Table 1. Summary of selected studies investigating animal personality and aggression.

Reference	Species	Aspect studied	Result
Carere et al. (2003)	*Parus major*	Post-conflict hormone changes	Post-contest stress response is dependent on behavioural type
Øverli *et al.* (2004)	*Onchorhyncus mykiss*	Links between behavioural and hormonal stress markers, aggression and dominance	Low stress individuals are more aggressive and dominant
Carere *et al.* (2005)	*Parus major*	Behavioural syndromes	High explorers use direct aggression but low explorers utilise other agonistic behaviours
Frost *et al.* (2007)	*Onchorhyncus mykiss*	Boldness; prior experiences and post-fight changes	Losing a fight decreases boldness; winning increases boldness.
Natarajan *et al.* (2009)	*Mus musculus*	Behavioural genetics, intra-individual variation	Consistent variation in aggression and agonisitc repertoire among strains
Wilson *et al.* (2009)	*Acheta domesticus*	Behavioural syndromes	Identified behavioural syndromes of mating, exploratory and antipredatory behaviour but not aggression or general activity.
Colléter & Brown (2011)	*Melanotaenia duboulayi*	Behavioural syndromes, dominance	Proactive individuals are more dominant
David *et al.* (2011)	*Taeniopygia guttata*	Behavioural syndromes, dominance	Proactive individuals are more dominant
Wilson *et al.* (2011)	*Xiphophorus helleri*	Repeatability of agonistic behaviour	Behavioural plasticity in relation to opponent RHP
Chang et al. (2012)	*Kryptolebias marmoratus*	Endocrine status and behavioural syndromes	Syndrome of boldness, aggressiveness and exploration; associated with pre-contest testosterone
Mowles *et al.* (2012)	*Pagurus bernhardus*	Behavioural syndromes	Behavioural syndrome of

|			boldness and investigation but not aggression.
Rudin & Briffa (2012)	*Actinia equina*	Boldness; contest outcome, post-fight changes	Boldness enhances RHP; losing reduces boldness
Jennings *et al.* (2013)	*Dama dama*	Intra-individual variation in contest escalation	Individuals with moderately predictable aggression have enhanced mating success
Wilson *et al.* (2013)	*Xiphophorus helleri*	Repeatability of agonistic behaviour	Repeatable aggressiveness; aggressiveness is an RHP trait
Favati *et al.* (2014)	*Gallus gallus domesticus*	Behavioural syndromes, dominance	Proactive individuals are more dominant
Courtene-Jones & Briffa (2014)	*Pagurus bernhardus*	Boldness; contest outcome, post-fight changes	Shyness enhances RHP for defenders; winning enhances shyness
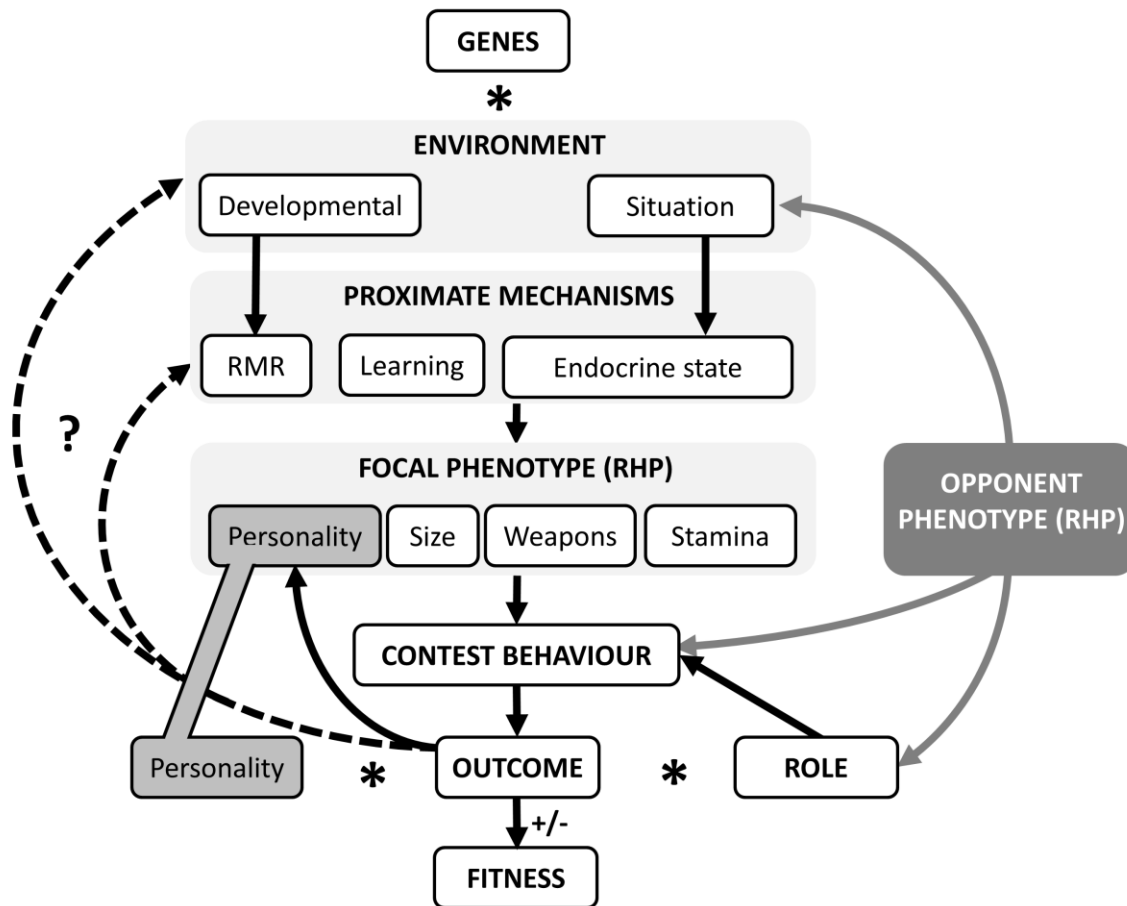
Figure 1: Proximate and ultimate links between personality and aggression, from the perspective of a focal individual, fighting an opponent. Solid lines: links demonstrated empirically. Broken lines: hypothesised mechanisms. * denotes interactions indicating that the effects of two components can be modified by one another.