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Environmental influence in animal contests

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Abstract

Contests between individual animals over the possession of particular limited resources have played an important role in shaping the evolution of life history, morphology and ecology of the vast majority of animal taxa. Whilst the phenomenon has been and continues to be extensively scrutinized via theory and experimentation, theses and predictions based on mathematics and optimality are frequently confounded by experimental observation. If successful demonstrations of evolutionarily stable strategies are to occur it is vital that the complex interplay of variables potentially affecting an animal's fighting ability are understood and controlled for experimentally. This review addresses the significance of external environmental influence on the decisions that animals make during conflict. With reference to the various game theory models and studies directly investigating the role of physiology in aggressive behaviour, this review calls for a collaboration between physiologists and behavioural ecologists in a hope of further understanding one of the fundamental selective processes in the evolution of motile animal taxa.

Resource holding potential and fighting behaviour

Examples of contests, involving two or more individuals competing directly for a limited resource, are found universally across the animal kingdom (Briffa & Elwood, 2009). Commonly contested resources include mating opportunities, access to food, territory and shelter (Arnott & Elwood, 2008). As fights seldom reach a point where one rival is physically unable to continue due to injury, conflicts are often resolved when one individual (usually considered the 'loser') makes the decision to leave the fight (MestertonGibbons, Marden, & Dugatkin, 1996). A 'winning' contestant, whether the fight has involved communication, assessments of strength (or morphological features) or injurious physical contact, will have more access to valuable resources-ultimately improving its chances of contributing genetic material to descendant generations. Animals capable of inducing a 'giving-up' decision in their rivals have demonstrated greater resource holding potential (RHP) than their opponent, and it is this difference in RHP which has frequently been viewed as a predictor of contest outcome (Taylor & Elwood, 2003).

Previous studies have revealed close correlations between an organism's RHP and body size or mass, with larger, heavier animals typically emerging as victor [e.g. Sand Goby *Pomatoschistus minutus*, (Lindstrom, 1992), Jumping Spider *Euophrys parvula*, (Wells, 1988); Pig *Sus scrofa*, (Rushen 1987)] due to a general assumption that size is related to strength (Archer 1988). However, when difference in body size is reduced, smaller animals do win fights more consistently (Huntingford, Taylor, Smith, & Thorpe, 1995), indicating that other important factors play a role in deciding an individual's RHP. Previous experience, position, sex, development of weaponry and motivation (e.g. presence of receptive females in the breeding season) have all been shown as predictors of contest outcome (Arnott & Elwood, 2009; Huntingford, et al., 1995). Indeed, it is likely that the results of all contests are governed by a suite of interacting traits, and whilst body size is successful as a proxy for RHP in some instances, it may be misleading or even contrary to apply it to all fights.

Before a contest is resolved, an animal must gather information about RHP on which to base its decision to persist or give up (Enquist & Leimar, 1983). Various game-theory models have examined the processes by which (it is presumed) individuals collect such information, and can be broadly grouped into two main types: self-assessment and mutual assessment.

Self-assessment models such as the war of attrition without assessment (WOA-WA) or energetic war of attrition (E-WOA) rely on the assumption that individual opponents only have access to information about their own RHP (MestertonGibbons, et al., 1996; R. J. H. Payne & Pagel, 1996), implying that a rival will give up when the cost of continuing to fight meets an individual absolute threshold; a threshold which has been determined by that contestant's RHP (MestertonGibbons, et al., 1996). Winners of contests in the straightforward WOA models are simply the individual whose RHP absolute threshold is higher and can therefore accrue more costs than the loser before giving up. WOA-WA and E-WOA models differ mainly in their interpretation of the relationship between energy spent and contest duration (MestertonGibbons, et al., 1996; R. J. H. Payne & Pagel, 1996).

Models falling into the mutual assessment category describe each individual basing its decisions on information about its own RHP as well as that of its opponent. This gives a contestant the advantage of being able to quickly end a conflict if the rival's

RHP is high relative to its own- before unnecessary costs are accrued in a contest it would eventually lose regardless (Briffa & Elwood, 2009). Popular theories include the asymmetric war of attrition (A-WOA) and sequential assessment models (SAM), both of which imply a strong degree of mutual assessment (Hammerstein & Parker, 1982; Parker & Rubenstein, 1981). RHP asymmetries are conveyed through sequences of agonistic behaviours which reveal information about a contestant's fighting ability (Hammerstein & Parker, 1982), ultimately culminating in the 'weaker' rival giving up. The SAM describes each behaviour in the sequence as a statistical sample, with fights escalating in intensity as more information is required (Enquist & Leimar, 1983). Thus low intensity behaviours employed early in conflicts are relatively 'unreliable' in the information about RHP that they carry, and if asymmetry proves to be low, more intense, 'reliable' behaviours- or 'samples'- are required for either rival to make the decision to give up (Parker & Rubenstein, 1981).

A third type of game theory model exists as a variation on the self –assessment forms mentioned above. According to the cumulative assessment model (CAM), animals gather information about their opponent's RHP through injuries or damage inflicted upon them (Robert J. H. Payne, 1998). No direct information about their opponent is available, and hence any individual fighting according to the CAM would still rely on reaching their absolute cost threshold before giving up (Payne 1998). As animals with higher RHP would inflict greater costs on their opponent, said threshold would be reached sooner than predicted by pure self-assessment models (Payne 1998).

An animal's resource holding potential may be said to be the result of a combination of sexual and natural selection, with traits that enhance ability being strongly selected for (Briffa & Sneddon, 2007). Some taxa where there are elevated levels of intrasexual conflict over mates, the choosier sex (often female) will pick mates with high relative RHP, selecting for increased agonistic performance across subsequent generations (Briffa & Sneddon, 2007). It is possible that physical characters that enhance RHP also increase attractiveness to potential mates (e.g. claw waving in Fiddler Crabs (Murai & Backwell, 2005), antler size and complexity in Red Deer (Clutton-Brock, Albon, Gibson, & Guinness, 1979)), indicating a likelihood that such morphology is sexually selected.

Whilst an individual's resource holding potential can be said to be hereditary due to selection for physical characters, it has also been shown in many taxa that other factors besides the animal's morphological attributes contribute to RHP and therefore fight success (review in Briffa and Sneddon 2007 and Arnott and Elwood 2009). Variations between conspecific individuals in terms of endocrine status, metabolic rate and energy reserves (for example) can therefore have direct effects on RHP.

Experimental evidence for physiological constraints on contest behaviour exists for several taxa (see table 1), but they are biased for small animals easily observed in laboratory studies (it becomes difficult to accurately measure energy expenditure for specific behaviours of large animals in the field). It is increasingly recognised that environmental factors influence an animal's behaviour (e.g. through interaction with energetics and metabolism (Huntingford, et al., 1995; Sneddon, Taylor, & Huntingford, 1999)) and due to the intrinsic energetic demands of contests, it is possible to assume that such influences are separable and quantifiable in agonistic

interactions. Environmental influences should be particularly prevalent in aquatic organisms, where osmoregulation and temperature have more direct effects on physiology than in terrestrial systems (Hay, 1996).

Costs of fighting- physiological demands and theoretical predictions

Aggressive interactions can be considered costly to the individual, be it through energy expenditure, time taken from other important activities, risk of injury (possibly leading to mortality) or predation risk (Briffa & Elwood, 2001; Glass & Huntingford, 1988) and an animal's decision to remain in conflict should be based on information gathered about such costs, adjusted for the perceived value of the resource (Arnott & Elwood, 2008). According to the 'hawk-dove' game (J. M. Smith & Parker, 1976), physical fighting with the possibility of injury is an evolutionarily stable strategy only when the cost of persisting is less than the perceived value of the resource, thus predicting that aggressive encounters where this was not the case would be ultimately settled by communication (J. M. Smith & Parker, 1976). Functions of repeated agonistic behaviours are explained differently by the various models (Robert J. H. Payne & Pagel, 1997), with mutual assessment models such as the SAM (Enquist & Leimar, 1983; Leimar & Enquist, 1984) assuming the key function is to provide a reliable display of the individual's RHP so that an opponent can make strategic decisions based on the costs already accrued.

Evidence that contest behaviour and outcome may be affected by energetic costs and physiological state has been reported for a variety of taxa (Table 1), with use of energy reserves, build up of harmful metabolites or endocrine status commonly being measured as a proxy for cost. With many animals, it is impossible to accurately measure the energy expenditure or vigour of a specific behaviour, so techniques have been developed which enable estimates or calculations to be made about energetic costs. Decapod crustaceans (particularly Portunid Crabs such as *Necora puber*, *Liocarcinus depurator* and *Carcinus maenas*) were popular early subjects for contest physiology experiments, and influential studies such as Smith and Taylor's (1993) experiment with the Velvet Swimming Crab *N. puber* used the beating of the ventilator pumps (the scaphognathites) as an indication of oxygen consumption. Whilst no significant difference in estimated consumption was found between contestants, the study revealed a highly elevated aerobic respiration experienced during the fight, a result that showed correlation with both the degree of escalation and duration of the interaction (I. P. Smith & Taylor, 1993). Similarly, Huntingford et al (1995) used scaphognathite activity to show that losers of *N. puber* contests would maintain the high level of aerobic respiration for longer than winners during the recovery period.

An alternative method for estimating cost is to approximately measure metabolic rate using respirometry. A study into ritualized male-male fights of the Sierra Dome Spider *Neriene litigosa* (DeCarvalho, Watson, & Field, 2004) used CO₂ respirometry to estimate mean and maximum metabolic rates during each of three identifiable separate phases of aggression, showing average (estimated) metabolic rate increase by factors of 3.5, 7.4 and 11.5 during the three phases respectively (DeCarvalho, et al., 2004). Hack (1997) used a similar technique to reveal a difference in energy expenditure between winners and losers of fights between members of the House Cricket species *Acheta domesticus*.

Table 1: Examples of physiological parameters examined for influence in animal contests.

Animal	Physiological parameter	Source
White Collared Dove <i>Streptopelia decaocto</i>	Physical (vocal) endurance	(ten Cate, Slabbekoorn, & Ballintijn, 2002)
Male Cichlid Fish <i>Tilapia zillii</i>	Depletion of sugar reserves; lactate build-up high in losers	(Neat, Taylor, & Huntingford, 1998)
Common Shore Crab <i>Carcinus maenas</i>	Elevation of heartbeat rate	(Rovero, Hughes, Whiteley, & Chelazzi, 2000)
Female Spiny Lizard <i>Sceloporous jarrovi</i>	Ovarian hormones regulate aggressive intensity	(Woodley & Moore, 1999)
Male House Cricket <i>Acheta domesticus</i>	Oxygen consumption extremely high during contest	(Hack, 1997b)
Red Jungle Fowl <i>Gallus gallus</i>	Testosterone levels prompt fight initiation	(Johnsen & Zuk, 1995)
Bot Fly <i>Cuterebra austenii</i>	Size-independent energy reserves predict contest winner	(Kemp & Alcock, 2003)
Wolf Spider <i>Hygrolycosa rubrofasciata</i>	Larger males incur higher metabolic costs from aggressive signalling	(Kotiaho et al., 1998)
Male Fiddler Crab <i>Uca lactea</i>	Blood glucose reserves low; lactate levels high post-contest	(Matsumasa & Murai, 2005)
Damselfly <i>Calopteryx maculata</i>	Winners contain higher fat content	(Marden & Rollins, 1994)

It was observed during the investigation that winners generally performed a “larger repertoire” of agonistic behaviours, resulting in higher energetic costs (Hack, 1997a). This finding illustrates not only the energetic costs of a fight, but also the implications that individual variations amongst animal metabolisms could affect their resource holding potential; a cricket with a weaker metabolism may not be able to meet the high energy demands required to win fights.

Briffa and Elwood (2001) used lactate and glucose concentrations in the haemolymph cavity of Hermit Crab *Pagurus bernhardus* to measure the build up of lactic acid and depletion of energy stores in individuals post shell-fight. Due to the nature of the contest (a series of bouts of shell ‘rapping’ that vary in intensity and duration), a measure of attack vigour could be made, and thus associated with the physiological costs. It was found that more vigorous bouts of rapping resulted in increased lactate levels, which subsequently constrained further bouts (Briffa & Elwood, 2001). As above, individual variation will drive contest outcomes not easily predicted by size or strategic position.

Further studies have consistently shown physiological demands associated with performing agonistic behaviours (Table 1). Physical endurance may prove a limiting factor in territorial disputes in the Great Tit *Parus major* (Weary,

Lambrechts, & Krebs, 1991), lactate concentrations in winners of fights between Copperhead Snake *Agkistrodon contortrix* returned to pre-fight levels within 60 minutes; significantly less time than in losers (Schuett & Grober, 2000), and claw waving in male Fiddler Crabs *Uca lactea* produced high levels of lactate even when individuals are prevented from coming into physical contact (Matsumasa & Murai, 2005). Physiological states can be affected by many interacting factors and an animal's RHP will depend on its individual capacity to effectively deal with increased metabolic rate, high concentrations of harmful metabolites or the requirement for increased aerobic respiration (amongst others). Here the interactions between environment and physiology are discussed, along with their implications for contest outcomes.

Environmental influence on physiological status and behaviour

An animal's physiology depends to a varying extent on the external environment which it inhabits (Domenici, Claireaux, & McKenzie, 2007). Aquatic organisms in particular are subject to physio-chemical pressures which limit both their geographical range and physical abilities (Claireaux & Lefrancois, 2007). Whilst deep sea habitats are subject to very little change in comparison to some terrestrial environments, shallow, coastal waters and freshwater systems vary greatly on both a predictable cyclical basis (seasons, tides, etc) and a more unpredictable scale (e.g. storms, pollution). This, however, is an effect not limited to aquatic environments, with all taxa in the biosphere subject to at least some influence from the external environment.

Some limiting properties of an animal's environment are intrinsic to the state of the medium in which it lives. Aquatic organisms experience viscosity and flow which can be viewed as physical constraints to biological and behavioural processes, and terrestrial organisms similarly experience wind. Other properties of environment such as oxygen and nutrient content (primarily in water) or temperature can have effects on an organism at tissue or organ level, which is reflected onto whole organism performance (Claireaux & Lefrancois, 2007; Domenici, Claireaux, et al., 2007), with implications for costly behaviours such as aggression.

The extent to which physical environmental factors affect an organism will vary fundamentally depending on the animal in question. Flow rates and viscosity will have much higher consequences for smaller planktonic species than free swimmers, and dissolved oxygen content will affect fish and crustacean metabolism, but not that of marine mammals and reptiles. Some species are adapted to deal with changing salinities and temperatures (e.g. estuarine organisms) and hence will not exhibit hindered performance under conditions of change to the same extent that species from a more stable environment would. Studies into the physiology of hypersaline diving beetles have revealed a link between salinity and ability to cope with temperature extremes (Sanchez-Fernandez et al., 2010) and further studies show that certain diving beetles (Coleoptera: Dytiscidae) exhibit behavioural responses to a change in temperature by surfacing more frequently and reducing mean dive duration (Calosi, Bilton, & Spicer, 2007).

Most studies into the impact of environmental variables on physiology focus on marine and aquatic animals, as often terrestrial environmental change on a

localised scale is both difficult to simulate experimentally and possibly ecologically irrelevant. The aquatic examples, however, offer insights into this phenomenon and implications for contest performance. Temperature has a clear and direct effect on muscle function in swimming Scup (Rome, 2007), showing longer relaxation and gait transition times at temperatures below 10C. Domenici et al. (2007) showed similar muscular effects of hypoxia during predator-prey interactions of several different marine fish species, with reduced activity and speed in avoidance of predators (Domenici, Lefrancois, & Shingles, 2007). Fish have been extensively studied in their reaction to hypoxia because of their high commercial value and the increasingly large areas of hypoxic waters in coastal regions as a result of eutrophication (Druon, Schrimpf, Dobricic, & Stips, 2004). Hypoxia has been shown to negatively affect fish metabolism (Lefrancois & Claireaux, 2003) and cardiovascular regulation (Fritsche et al., 1993), which ultimately lead to reduced activity (as above) and growth (Eby, Crowder, McClellan, Peterson, & Powers, 2005).

Environmental conditions may also affect sensory apparatus used in activities such as foraging, predator avoidance or contests. Adult Atlantic cod *Gadus morhua* are one of a number of predatory fish relying mainly on vision for navigation and prey capture, and a recent study has shown a decrease in activity at intermediate turbidities, followed by an energetic cost-heavy increase in activity at high turbidities as the adults ramp up their effort to find prey (Meager & Batty, 2007). Alien noise and scent will inevitably have similar effects on animals relying on olfactory or sonic senses.

Implications for contest behaviour and RHP

Using examples of environmental effects on physiology and behaviour, if viewed in conjunction with physiological studies of animal contests, inferences can be made about the direct and indirect effects of environmental variation on fight performance and resource holding potential. Agonistic behaviours are costly, in terms of time taken from other important activities, depletion of energy reserves, injuries sustained or predation risk. A contestant's capacity to endure these costs can make the difference between 'winning' and 'losing' a fight, particularly according to self-assessment models such as the cumulative assessment model or the energetic-war-of-attribution. During contests where movement and strength are important (e.g. opercular displays in Siamese Fighting Fish; grappling in Shore Crabs), muscular development and stamina will enhance a contestant's relative RHP. According to studies by Domenici et al. (2007) and Lefrancois and Claireaux (2003), both temperature fluctuations and reduced oxygen concentration have adverse effects on locomotion and recovery time from activity. The authors refer to escape from predators and foraging as being primarily affected in the examined species, but costly behaviours involved in those activities will be closely linked to behaviours used in aggressive interactions. An individual of the Siamese fighting fish species *B. splendens* of a given size that has been exposed to low temperatures or reduced oxygen concentrations may exhibit a lower strength or endurance threshold than would be estimated by size alone.

Similarly, the schaphaghonathite beating used by Smith and Taylor (1993) to estimate oxygen consumption during *N. puber* fights indicates a greatly increased level of aerobic respiration during contests. *N. puber* inhabits coastal regions and intertidal zones (Lee, Coleman, & Jones, 2006) and as such may be subject to the

lowered dissolved oxygen concentrations that would be present in rockpools or fully exposed substrate. A fight between two *N. puber* individuals where the immediate chemical histories differed (i.e. one contestant has just entered the water after an extended exposed period) would incur an RHP asymmetry unpredicted by present theories due to the lowered metabolic rate and potential muscular inadequacies of the disadvantaged rival. A study by Briffa and Elwood (2000) utilises the idea of hypoxic fatigue to test the sequential and cumulative assessment models in fights over gastropod shell ownership of the hermit crab *Pagurus bernhardus*. Crabs were subjected to periods of reduced oxygen intake before contests were staged. The authors found that whilst attacking individuals reduced the vigour and duration of signal bouts, defending crabs were seemingly unaffected by hypoxia in the context of the fight (Briffa & Elwood, 2000). This not only implies a notable effect of hypoxia on the attacking crab, but also the advantage given to the defender by position at times of lowered oxygen concentration.

Game theory models predicting mutual assessment such as the sequential assessment model or the asymmetric-war-of-attrition rely on the concept that both opponents will be evaluating the other's RHP through a series of escalating phases of conflict. Crucial to this idea is the ability of the individuals to accurately gather information. Fights displaying properties similar to either of these models would be directly affected by environmental changes that hinder or improve sensory ability.

An animal's environment extends beyond simply the physical properties of their surroundings to include the distribution and abundance of conspecifics and other taxa that share the habitat. In the above example of hermit crab fights, the position of the defender ensures an unchanged RHP relative to the attacker's, and it has been shown that Swimming Crab *N. puber* will fight with more intensity and for longer in the presence of receptive females during the breeding season, contrary to previously assumed predictors of fight success such as body size (Huntingford, et al., 1995).

Conspecifics that are close enough to observe a fight have been shown to modify their behaviour when interacting with either winners or losers (Mesterton-Gibbons & Sherratt, 2007). This 'social eavesdropping' is a recent theory explaining how weaker animals can avoid conflict by comparing the costs of engaging in agonistic interactions with a known winner (and the likelihood of losing) with the potential benefit of winning. A study into this theory revealed that eavesdropping in Green Swordtail fish *Xiphophorus helleri* indeed produced a significant reduction in the bystander's propensity to engage in conflicts with known winners, and when such conflicts did rarely arise, the proportion of wins against winners was also reduced (Earley & Dugatkin, 2002). This result was reported despite variations in size and estimated strength which originally thought dictated fighting ability.

It is unclear how often in nature the circumstance would arise of two contestants in a fight possessing different immediate histories which would affect physiology, or how sensory effects could hinder one contestant and not the other. It is clear, however, that environment influences an animal's behaviour and the strategic decisions it makes during a fight through the chemical and physical properties of said environment or the spatial distribution of other organisms. Effects of

environmental variation depend on the fighting type of the individual, and can be predicted by examining the various game theory models. Incorporating environmental factors into behavioural studies of aggression will help reveal proximate reasons how the energetic costs of contests constrain, and how external variation can alter RHP by limiting or augmenting the intensity of agonistic behaviours and the information gathered by rivals.

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