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Mark Briffa
Plymouth University

Lynne U. Sneddon
University of Liverpool, lsneddon@liverpool.ac.uk

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Physiological constraints on contest behaviour

M. BRIFFA*† and L. U. SNEDDON‡

*Marine Biology and Ecology Research Centre, University of Plymouth, The Davy Building, Drake Circus, Plymouth PL4 8AA, UK, †University of Liverpool, School of Biological Sciences, The BioScience Building, Liverpool L69 7ZB, UK

Summary

1. Contests may involve injurious fighting, other types of direct physical aggression and communication. They occur over ownership access to mates and other resources that may increase an individual's attractiveness and its chance of survival. Traits that enhance resource holding potential may be the result of sexual selection, natural selection or a combination of both.

2. Agonistic behaviours are expected to be demanding to perform and costly in terms of changes in physiological state. The ability to meet the physiological costs may determine contest outcomes and constrain the intensity of agonistic activities.

3. The energetic costs have been investigated in a broad range of taxa using a variety of techniques. They include the mobilization of energy reserves, but a key cost in several taxa appears to be limited anaerobic capacity and subsequent accumulation of lactic acid. Androgens, stress hormones and neurohormones have also been shown to constrain fighting behaviour. However, due to key differences in the endocrine systems of vertebrates and invertebrates, the effects of hormones are far less consistent across taxa than in the case of metabolites.

4. Physiological constraints on fighting may vary according to their importance relative to circumstantial costs, the time-scale over which they exert their effects, their effects on different roles and their causal links with behaviour. Incorporating these factors into theoretical studies of contest behaviour may give further insights of how the costs of fighting influence agonistic behaviour.

Key-words: fighting, hormones, metabolism, proximate-costs, sexual competition

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Animal contests and resource holding potential

The idea that sexually selected traits, such as large body size, conspicuous ornaments or behavioural patterns, should be costly is predicted by theory (Zahavi 1977; Grafen 1990) and supported by empirical evidence (e.g. Kotiaho *et al.* 1998). It is intuitive that such traits may be used to attract mates directly but they may also lead to enhanced mating opportunities when used in competitive interactions between rivals over access to mates. Animals may fight over many types of resource but mating opportunities may be thought of as the most highly prized resource that sexually reproducing animals compete over. Where a conflict occurs over a restricted resource, animals usually settle the dispute by engaging in a 'contest' consisting of 'agonistic' behaviours. Contests may involve dangerous fighting

with injuries or fatalities (e.g. male Elephant Seals, *Mirounga angustirostris*, Haley 1994), 'trials of strength' (e.g. Red Deer *Cervus elephas*, Clutton-Brock & Albon 1979), communication (e.g. Pompilid Wasps, *Hemipepsis ustulata*, Kemp & Alcock 2003) or a combination of these. Regardless of how the contest is settled the function of agonistic activities is ultimately to cause the 'withdrawal of a rival or opponent' (Huntingford & Turner 1987), in other words to induce the opponent to make a decision to 'give up'. Therefore, selection should favour individuals that invest in resources that increase their relative 'fighting ability' because this will allow them to gain more mating opportunities than their rivals. An individual that wins a contest by causing its opponent to withdraw has demonstrated superior fighting ability or 'resource holding potential' ('RHP') relative to its opponent.

Engaging in fights is expected to be costly. Factors such as loss of time available for other activities or increased risk of predation are circumstantial costs of

fighting but other costs such as injuries, depletion of energy reserves or a change in endocrine status are intrinsic to the agonistic activities used in the fight. If these costs are sufficiently high they may constrain the intensity of agonistic behaviour and influence the strategic decisions made during fighting. Many features that vary between individuals are therefore likely to contribute to RHP. As noted above, many species are sexually dimorphic in terms of body size (review in Andersson 1994) and this has long been considered a key 'correlate of RHP', such that fighting ability increases with size. There may also be strong selective pressure on traits that are used as weapons or signals. Thus, in addition to size, an individual's capacity to use weapons or perform signals may also correlate with RHP.

One means of investigating such capacities is to assess 'whole organism performance' of an ecologically relevant task. These may relate to endurance capacity (= 'stamina'), in the case of tasks such as forced locomotion, where the total distance covered before exhaustion can be measured (e.g. Irschick & Garland 2001; Lailvaux *et al.* 2005), or to 'strength' in the case of tasks such as biting, pinching with claws or wrestling where force generation can be measured (e.g. Sneddon *et al.* 2000a, Lailvaux *et al.* 2005; Husak *et al.* 2006). As strength and endurance capacity are likely to be important during contests an individual's capacity in these respects during other situations should correlate with their ability to win contests.

An alternative approach is to measure changes in physiological state that occur as a result of fighting. Investigation of energy metabolism, for example, may involve respirometry or the quantification of ventilatory or cardiac rates. In addition, post-fight assays of metabolite levels or circulating hormones can be compared with levels at rest or following exercise and between winners and losers of contests. The intensity of agonistic behaviour can also be compared with these physiological measures in cases where the intensity can be accurately quantified (e.g. shell rapping in Hermit Crabs, claw waving in Fiddler Crabs, roaring in Red Deer). In some respects the intensity of agonistic behaviour is another measure of 'whole body performance' similar to the examples mentioned above. An important difference, however, is that during fights an individual's behaviour is likely to be influenced by that of its opponent and by its motivational state (the value of the resource) and therefore may not accurately reflect performance capacities. Measurement of contest energetics and hormone levels, on the other hand, allows relationships between physiological state and the intensity of agonistic performance to be examined. It is thus possible to determine whether the proximate physiological costs of demanding activity (e.g. use of energy reserves, accumulation of harmful metabolic by-products or a change in hormonal state) constrain the intensity of agonistic behaviour (often referred to as 'fight-performance') and influence strategic decisions.

Selection for resource holding potential or attractiveness?

Where competition over mates is prevalent and the opposite sex chooses the fittest partners with superior traits, selection for high RHP will be strong and we may expect to see particularly high rates and intensity of contest behaviour. In such situations, however, correlates of RHP may also be used as measures of quality by potential mates, usually with 'choosy' females assessing the quality of competitive males. Furthermore, intrasexual contests may be a mechanism that allows assessment of quality by the choosy sex. Therefore, investment in traits such as large body size, strong weapons, and endurance capacity may increase attractiveness in addition to RHP. Usually, having a greater RHP ensures an individual is the victor in contests and indeed in many cases larger males secure more matings, e.g. in Shore Crabs *Carcinus maenas* (Reid *et al.* 1994).

Where sexual dimorphism is prevalent empirical evidence has shown that in most cases larger males win fights over females and other resources (Huntingford *et al.* 1995; Neat, Huntingford & Beveridge 1998a; Petersson *et al.* 1999; Sneddon *et al.* 2003), although factors other than size can also play an important part. In some cases small males can adopt alternative tactics (e.g. lizards, Wikelski *et al.* 1996; Zamudio & Sinervo 2000; fish, Oliveira *et al.* 2001a; Locatello, Mazzoldi & Rasotto 2002; Aubin-Horth *et al.* 2005) and features such as manoeuvrability in the midge *Chironomus plumosus* (Neems, McLachlan & Chambers 1990) or lipid reserves in the damselfly *Calopteryx maculate*, may also influence outcomes. In some cases, such as the lizard *Anolis carolinensis* (Jenssen, Decourcy & Congdon 2005), motivation may play an important part such small males may initiate and even win fights more often than predicted by variation in size. Furthermore, where both sexes are competitive and/or females compete for access to males, differences in RHP traits between the sexes are not normally apparent ('monomorphism') (e.g. capuchinbirds and lekking species, Trail 1990; Pinyon Jays *Gymnorhinus cyanocephalus*, Johnson 1988, Convict Cichlid fish, *Cichlasoma nigrofasciatum*, Beeching *et al.* 1998).

It is clear, then, that many traits associated with RHP (perhaps body size in particular) may also function in increasing attractiveness to potential mates and that sexual selection must play a key role in the evolution of contest behaviour. On the other hand, some traits associated with high RHP may reduce attractiveness; it has been shown in several species, for example, that females actually avoid mating with males of high RHP in order to avoid injuries (Wong & Candolin 2005). Furthermore, it is also important to note that contests also occur for resources other than mates and that males and females may compete for the same resource. In such cases, a contestant's sex may also contribute to its RHP as has been shown in the Hermit

Crab *Pagurus filiohi* where males out-compete females during contests over empty gastropod shells (Yoshino & Goshima 2002), and in fish such as Convict Cichlids, *C. nigrofasciatum* (Koops & Grant 1993) and Coho Salmon, *Oncorhynchus kisutch* (Holtby, Swain & Allan 1993). The causes of these intersexual differences in RHP are unknown, but may be due to factors such as differences in energy reserves available for use in contests. Gametogenesis, for example, is usually more costly for females so they may devote less energy to fighting. Further, differences in hormonal state may cause differences in RHP between the sexes. These possibilities could be examined both by investigation of performance capacities and by assay of physiological status with respect to sex, contest outcomes and intensity of agonistic behaviour.

Costs of fighting and theoretical predictions

Theoretical analyses suggest that many contests, regardless of the contested resource, the types of agonistic activities used or whether they occur inter- or intrasexually, should involve the use of demanding activities that are costly to perform. 'Evolutionary game theory' shows how the costs of fighting (C), the value of the resource (V) and the activities of the opponent determine the types of agonistic activity that should be used to settle a contest. An early prediction from the basic 'hawk-dove' game (Maynard Smith & Parker 1976) is that dangerous fighting is only an evolutionarily stable strategy (ESS) when $C < V$. Under all other conditions we should expect to see a proportion of contests settled by communication. Further developments allowed the inclusion of asymmetries in RHP, resource value and other factors such as resident-intruder effects where the resident usually wins (Table 1).

The Sequential Assessment Model (SAM) (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist 1985; Leimar, Austad & Enquist 1991) has been extremely influential as it accounts for the observation that in many cases contests escalate through a series of phases of increasing intensity. In this model, it is assumed that a key function of agonistic activities is to enable the opponent to assess the performer's RHP as accurately as possible such that within a phase activities are performed at a constant level (e.g. in the Cichlid Fish *Nannacara anomala*, Enquist *et al.* 1990). On the other hand, accurate assessment may not always be possible and the War of Attrition (WOA) model was proposed whereby animals progressively increase the level of agonistic behaviour from low cost display to more costly physical contact and finally escalating to injurious fighting (Bishop & Cannings 1978; Hammerstein & Parker 1982). At each step, the opponents obtain more reliable information about RHP and can decide to retreat at any point during the contest. The winner will then be the individual prepared to devote the greatest amount of time or energy to the contest.

Recent developments question the occurrence of such 'mutual assessment' and suggest that in some cases the assessment capabilities of fighting animals may be limited to 'knowing' or assessing their own ability or state (Taylor & Elwood 2003; reviewed by Gammell & Hardy 2003). Thus, decisions are made on the basis of an individual's own level of accumulated costs rather than in relation to the costs accrued by the opponent. Although this type of fighting is probably not possible under models such as the SAM that rely on mutual assessment, it is congruent with alternative models such as the WOA in its original and 'energetic' version (EWOA) and with the Cumulative Assessment Model (CAM) (Payne 1998). The various models suggest different functions for agonistic activities, in terms of how they affect the 'withdrawal of a rival or opponent'. Payne & Pagel (1997) compare the different functions of repeated agonistic activities and show how the different models make different predictions about (1) change in the pattern of agonistic behaviour during contests, and (2) the rate of accrual of costs during contests. Here we will consider how (1) the energetic costs of agonistic behaviour, and (2) variation in endocrine status have been linked to fight outcomes and how the intensity of agonistic behaviour may be linked to these physiological constraints.

Energetic constraints on agonistic performance

The first evidence that contest behaviour may be constrained by the energetic costs of performance is given by Clutton-Brock & Albon's (1979) study of Red Deer *C. elaphus*. These contests escalate through a series of phases of increasing intensity from 'roaring' signals, to parallel walking and finally antler pushing with a very small proportion of encounters involving injuries. This pattern of escalation from signals, through a 'trial of strength' and finally to injurious fighting is typical of many animal contests. A proportion of the contests are settled at the signalling stage and anecdotal evidence of exhausted males collapsing after contests suggests that the intensity and duration of the roaring signals is constrained by the energetic demands. Endurance capacity may similarly limit the use of acoustic signals during contests over territory in birds such as the Great Tit *Parus major* (Weary, Lambrechts & Krebs 1991) and White Collared Dove, *Streptopelia decaocto* (ten Cate, Slabbekoorn & Ballintijn 2002) and in anurans (Ryan 1988).

Direct measurement of the energy expenditure of fighting is difficult to achieve in large animals and during naturally occurring contests in the field. Thus, although it is increasingly recognized that environmental variables should influence behavioural decisions, for example as a result of interactions with energetic constraints (e.g. Sneddon, Huntingford & Taylor 1998; Sneddon, Taylor & Huntingford 1999a,b; Briffa & Elwood 2000), relatively few studies have attempted this (but see Dearborn, Anders & Williams

Table 1. Examples of asymmetries used to settle animal contests that are linked to reproductive success and may be important in sexual selection

Asymmetry	Animal	Cue/resource	Reference	
RHP	Lizard, <i>Anolis carolinensis</i>	Body size	Jenssen <i>et al.</i> (2005)	
	Varanid Lizards	Body size	Earley, Attum & Eason (2002)	
	Squid <i>Loligo plei</i>	Body size	DiMarco & Hanlon (1997)	
	Brown Trout <i>Salmo trutta</i>	Body size	Petersson <i>et al.</i> (1999)	
	Copperheads <i>Agkistrodon contortrix</i>	Body size	Schuett (1997)	
	Shore Crabs <i>Carcinus maenas</i>	Weapon size and strength	Sneddon <i>et al.</i> (1997, 2000a)	
	Fiddler Crab <i>Uca perplexa</i>	Weapon size	Murai & Blackwell (2005)	
	Lizards	Weapon strength		
	<i>Anolis carolinensis</i>		Lailvaux <i>et al.</i> (2004)	
	<i>Gallotia galloti</i>		Huyghe <i>et al.</i> (2005)	
	<i>Crotaphytus antiquus</i>		Husak <i>et al.</i> (2006)	
	Cockroaches <i>Gromphadorhina portentosa</i>	Hiss frequency	Clark & Moore (1995)	
	Crickets <i>Gryllus bimaculatus</i>	Mandible spreading	Hofmann & Schildberger (2001)	
	Widow Birds <i>Euplectes ardens</i>	Red collar intensity	Pryke, Lawes & Andersson (2001)	
	Firemouth Cichlids <i>Cichlasoma meeki</i>	Red mouth intensity	Evans & Norris (1996)	
	Butterfly, <i>Pararge aegeria</i>	Body temperature	Stutt & Willmer (1998)	
	Damselfly <i>Calopteryx maculata</i>	Fat reserves	Marden & Waage (1990)	
	Resource value	Snapping Shrimp <i>Alpheus angulatus</i>	Possession of females	Mathews (2002)
		Golden Orb Spider <i>Nephila fenestrata</i>	Possession of females	Fromhage & Schneider (2005)
		Pygmy Sunfish	Hunger	Parker & Rubenstein (1981)
Shrews		Hunger	Barnard & Brown (1984)	
Crickets <i>Acheta domesticus</i>		Hunger	Nosil (2002)	
Swordtail Fish <i>Xiphophorus helleri</i>		Environmental richness	Nijman & Heuts (2000)	
Robins <i>Erithacus rubecula</i>		Territory value	Tobias (1997)	
Resident-intruder (owner wins)		Sparrows	Prior residency	Snell-Rood & Cristol (2005)
		<i>Zonotrichia albicollis</i> Seabream <i>Diplodus sargus</i>	Prior residency	Caballero & Castro (1999)
Combination of above factors		Elephant Seals <i>Mirounga angustirostris</i>	Prior residency and body size	Haley (1994)
	Crab Spider <i>Misumenoides formosipes</i>	Prior residency and prior fight experience	Hoefler (2002)	
	Fiddler crab <i>Uca annulipes</i>	Prior residency and weapon size	Jennions & Backwell (1996)	

2005). Therefore, most studies of contest energetics have been based on staged encounters in species amenable to study in the laboratory.

Portunid Crabs, *N. puber*, *Liocarcinus depurator* and *C. maenas*, were early subjects for investigating the physiology of contest behaviour and have remained important model species. Huntingford *et al.* (1995) provide a detailed description of the agonistic activities, which involve displays, physical grappling

and occasionally injurious fighting. Smith & Taylor (1993) found significantly elevated rates of scaphogathite (gill bailer) beating during agonistic activities in *N. puber* and demonstrated a positive association between contest duration and the level of elevated beating. Interestingly, elevated scaphogathite beating was found not only during phases of physical contact between the opponents but also during the use of display activities. The level of advertisement given by such

displays may correlate with claw size because it could act as an index of body size but this association with scaphognathite beating indicates that they are also associated with an elevated metabolic rate. Rovero *et al.* (2000) similarly found elevated heartbeat rates during fights in *C. maenas*, again indicating increased energy expenditure with increasing contest duration.

Conversely, neither study detected any relationship between energetic costs and contest intensity indicating that the costs associated with the agonistic activities are not sufficiently high to constrain the level of performance. Indeed, both studies concluded that fighting is less costly than forced exercise. In *C. maenas*, however, the costs appeared to be higher for losers than winners because they showed increased rates of ventilation during the contests and during a post-contest recovery phase, whereas post-contest elevation was not seen in winners. Thus, although the energetic demands may not influence the intensity of agonistic behaviour in this case, they may be related to the decision of losers to give up.

An alternative approach to estimating the costs of performance during a fight is to use respirometry to estimate metabolic rates. Brown *et al.* (2003), for example, found that contests over dominance in the freshwater prawn *Macrobrachium rosenbergii* were won by individuals with a high resting metabolic rate, independent of the effects of body size on metabolism, indicating a clear effect of individual quality on RHP. If the average metabolic rate of a given activity is known the energy expenditure for each opponent can be estimated by extrapolating from behavioural observations. This approach was used by Hack (1997a, 1997b) in studies of fighting in male House Crickets *Acheta domesticus*. As in Portunid Crabs, contests involve a range of different tactics of varying intensity (Hack 1997b) including physical interventions such as biting, head butting and kicking in addition to signals such as stridulation, mandible flares and rocking. Oxygen consumption increased with fight duration at a greater rate for winners than for losers such that net oxygen consumption per contest was greater in winners. Furthermore, regardless of victory, fights in House Crickets appear to be considerably more demanding than other activities, respiration rates being five times greater during fights than at rest. Similar effects on respiration rates are seen during male–male fights in the Sierra Dome Spider *Neriene litigiosa* (DeCarvalho, Watson & Field 2004). Energy expenditure increases as the contest escalates in intensity, through three distinct phases, displays (3–5 times above resting), wrestling and biting (in excess of 11 times greater than at rest). In both crickets and spiders it is clear that the metabolic rate during fights varies according to the tactics employed and the rate of accrual of energetic costs may be a source of asymmetry between the opponents and may determine the choice of tactics adopted in the contest (Grafen 1990; Hack 1997a).

The studies on crickets highlight a potential problem with applying the concept of ‘handicaps’ to signals used during contests. The handicap principle (Zahavi 1977) is based on the idea that costs associated with signals should accrue more quickly for individuals of low quality than for individuals of high quality (see Hurd 1997) but in these encounters winners show a greater metabolic rate than do losers indicating that their energy reserves are depleted more quickly. One possible explanation for this apparent contradiction is that contests are not necessarily settled by the use of signals alone and this is certainly true in *A. domesticus* encounters. A second explanation given by Hack (1997a) is that although winners use energy reserves at a higher rate, the loss of energy could have a greater impact on the fitness of losers if they are poor quality individuals with lower reserves. Thus, although winners pay higher costs during the contests the fitness cost is actually greater for losers.

If fight tactics and strategic decisions are constrained by metabolic costs then we should expect to see (1) relationships between fight intensity and post-fight energetic status, and (2) differences in post-fight energetic status between winners and losers. In intra-sexual contests in many insects, older males with greater energy reserves persist for longer and are more likely to win than younger males (Convey 1989; Marden & Waage 1990; Marden & Rollins 1994; Plaistow & Siva-Jothy 1996; Kemp 2002; Kemp & Alcock 2003). This observation supports the EWOA model that predicts that the contestant willing or capable of assigning the greater amount of energy to the contest will win. In *N. puber*, however, post-fight assay suggests that there is no effect of fighting on the levels of haemolymph glucose and tissue glucose and glycogen levels (Thorpe, Taylor & Huntingford 1995). In contrast, forced exercise appears to cause significant mobilization of muscular glycogen reserves. In *C. maenas* fighting results in elevated haemolymph glucose levels compared with resting levels (Sneddon *et al.* 1999a). Elevated glucose is also seen during fights in the common European Hermit Crab *Pagurus bernhardus* during fights over empty gastropod shells (Briffa & Elwood 2001a). These fights involve two distinct roles with ‘attackers’ repeatedly performing vigorous bouts of shell-rapping signals (see Briffa, Elwood & Dick 1998) and ‘defenders’ remaining withdrawn into their shells for most of the encounter. This repeated shell rapping is an example of ‘agonistic performance’ that can be accurately quantified in terms of its intensity, as the activities of the defender appear to have a minimal effect on the behaviour of the attacker during the bouts of activity. Defenders that resist being evicted from their shell have higher circulating glucose levels than evicted defenders (Briffa & Elwood 2001b) and a greater proportion of their muscular energy reserves mobilized as glucose rather than stored as glycogen (Briffa & Elwood 2004) but there are no differences between successful and unsuccessful attackers. Thus,

in these contests where there are two distinct roles, the use of energy reserves does seem to be associated with the giving up decision but only for one of the roles.

Elevated glucose appears to be a feature of contests in crustaceans and mobilization of energy reserves may be partly responsible for depleted muscular glycogen seen in fighting decapods (Thorpe *et al.* 1995; Sneddon *et al.* 1999a; Briffa & Elwood 2004). However, glycogen stores may also be depleted directly via anaerobic respiration and investigations of the effects of hypoxia on fighting indicate that this may be the case. In *C. maenas* under normoxic conditions, fighting results in significant elevation of circulating glucose but not to the extent seen in crabs that have undergone forced exercise. In hypoxic conditions, however, the level of elevation exceeds that seen in exercised crabs, and the fights are of shorter duration (Sneddon *et al.* 1999a,b) and decreased fight vigour under hypoxia has been shown during shell fights in *P. bernhardus* (Briffa & Elwood 2000). In fish the use of 'opercular displays', where the gill covers are flared while facing the opponent, are seen during contests in many species. In Siamese Fighting Fish, *Betta splendens* (Abrahams, Robb & Hare 2005) shows that display rate is severely reduced under hypoxic conditions. Opercular displays may advertise body size but they are also known to disrupt the respiratory flow of water through the gill chambers. They may therefore serve a secondary function of advertising resistance to lactate accumulation by imposing a period of anaerobic respiration on the sender.

Increased rates of oxygen consumption indicate that fighting is demanding (Smith & Taylor 1993; Rovero *et al.* 2000; Hack 1997a,b, DeCarvalho *et al.* 2004) and must be fuelled by elevated rates of aerobic metabolism. Although there will be an associated cost of increased energy consumption (Sneddon *et al.* 1999a,b; Briffa & Elwood 2001a, 2004), this may not be sufficient to act as a constraint on performance, unless the energetic demands exceed available energy reserves. A key feature of crustacean physiology is a limited capacity for aerobic metabolism such that a proportion of the demanding contest behaviour may be fuelled by anaerobic respiration. The resultant accumulation of lactic acid, in addition to the depletion of glycogen reserves, could then represent a serious additional cost of fighting by constraining post-contest activity rates and, during protracted encounters, could constrain levels of performance during the contest.

Studies on *N. puber* (Thorpe *et al.* 1995) indicate that fighting did not cause a significant increase in circulating lactate levels but significant elevation was seen in crabs subjected to forced exercise to exhaustion. In *C. maenas* elevated lactate is seen as a result of fighting, although as in the case of *N. puber*, fighting appears not to be as demanding as forced exercise (Sneddon *et al.* 1999a). In both species, there was no difference in the concentration of lactic acid between

winners and losers. This indicates that rather than constraining the ability of losers to continue in the fight, lactate accumulation may represent a cost in terms of the post-contest time required to recover from the oxygen debt accrued during the encounter. Until they have recovered their capacity for other activities will be constrained such that lactate accumulation may have a negative impact on fitness. Although there is no difference in lactate between winners and losers, rates of recovery could vary between individuals. Perhaps then the activities used during Portunid Crab fights advertise RHP in a similar manner to the activities performed by fighting crickets.

Significant lactate accumulation as a result of agonistic activity has been demonstrated in a range of crustaceans including male Fiddler Crabs *Uca lacteal perplexa*. (Matsumasa & Murai 2005) show that haemolymph lactate increases while the rate of agonistic claw waving signalling declines. A similar result is seen during shell fights in Hermit Crabs but in this case there are differences between the two roles and with contest outcomes. In both attackers and defenders lactate increases as a result of fighting (Briffa & Elwood 2001b, 2002) but in attackers only there is a significant increase with increasing contest duration (Briffa & Elwood 2005). There is also an associated decline in the vigour of shell rapping from bout to bout but only in attackers that fail to evict the defender, who perform fewer raps in each bout at the end of fights. Successful attackers increase the number of raps from bout to bout until the defender gives up (Briffa *et al.* 1998; Briffa & Elwood 2002). Furthermore, in attackers that give up (losers) post-fight lactate is greater than those that effect an eviction (winners) and in all attackers, regardless of the outcome, there are negative relations between the vigour of shell rapping and lactate concentration (Briffa & Elwood 2002; Briffa & Elwood 2001a). In this case it therefore appears that the cost of accumulated lactate constrains the performance of attackers during the fight. As losers have higher lactate than winners there is also the possibility that the cost is either more severe or accrues more rapidly for poor quality individuals. Indeed, detailed behavioural studies of changes in the pattern of shell rapping (Briffa *et al.* 1998; Briffa & Elwood 2000) during encounters suggest that shell rapping may advertise the stamina of attackers in a manner similar to that predicted by the energetic war of attrition model E-WOA.

It appears that in crustaceans, which are particularly limited in terms of aerobic capacity, lactate accumulation is a significant cost of contest behaviour, but it may also play a significant part in a wide range of taxa, including vertebrates. Abraham *et al.*'s (2005) study on *B. splendens* indicates that lactate accumulation could have a significant role during contests, and Brandt (2003) similarly found that threat displays in the lizard *Uta stansburiana* impaired aerobic respiration resulting in elevated post-fight lactate. Interestingly, the duration of these displays was associated with a

post-display decrease in endurance capacity as evidenced by performance of running on a treadmill. Neat, Taylor & Huntingford (1998b) show that muscular glycogen reserves are depleted anaerobically during fights in the Cichlid Fish *T. zillii* resulting in elevated lactate and higher lactate was seen in losers than in winners. Another vertebrate example is Schuett & Grober's (2000) study of Copperhead Snakes *Agkistrodon contortix*, where losers but not winners show elevated lactate compared with resting levels. Thus, elevated lactate appears to be an important consequence of fighting that is linked to performance capacities across a broad range of taxa and in some cases may be a causal factor for the decision to give up.

Hormonal constraints on agonistic performance

Hormonally driven changes in physiology can have a profound effect upon aggressive behaviour particularly during the breeding season where surges in androgens can enhance the motivation to engage in agonistic encounters when males are contesting access to females. The classic example of hormone driven aggression is that of the castrated rodent where the reduction in testosterone by removal of the testes reduces the frequency of aggressive attacks. A variety of hormones are released from the endocrine system that can have direct and indirect effects upon aggression in both the developing and adult individual (see Huntingford & Turner 1987 for a selection of hormones and their effects on fighting ability). Studies have linked hormones with fight motivation and outcome but specifically three classes: the androgens; the stress hormones; and the neurohormones such as biogenic amines. Hormonal changes have been recorded in Cichlids simply watching other males fights (Oliveira *et al.* 2001a,b), thus hormones are instrumental in both in the preparation for fighting and show an elevation during and after contests (e.g. Californian Mice, *Peromyscus californicus*, Oyegbile & Marler 2005).

Most research has targeted the reproductive hormones in vertebrates as competition for access to reproductive opportunities is linked to increased aggression and major changes in behaviour such as the establishment of a territory, building of a nest, changes in coloration (e.g. male Threespined Stickleback, *Gasterosteus aculeatus*, becomes highly aggressive, territorial, and develops red throat coloration; Wootton 1976). Indeed, androgens have shown strong relationships with aggressive state in a variety of vertebrates where male–male competition occurs over females. In the Red Jungle Fowl, *Gallus gallus*, males that initiated and won fights had much higher testosterone levels relative to their opponent (Johnsen & Zuk 1995). However, the effects of androgens can be less perceptible as seen in *Tilapia zillii*. Even though relative gonad size is related to winning, testosterone does not correlate with agonistic success (Neat & Mayer 1999). Other studies have examined the behavioural consequences

of castration and thereby reducing testosterone in males and found that this directly reduces agonistic behaviour (Huntingford & Turner 1987). In contrast, many studies have used implants to experimentally increase hormone levels and have shown that male traits, courtship behaviour and aggression are increased. In male Red Grouse, *Lagopus lagopus*, their sexual ornaments, the red comb, became larger coupled with an increase in aggressive call rate when given testosterone implants demonstrating a causal relationship (Mougeot *et al.* 2005). However, when competition for females is indirect or resources need to be acquired such as shelters or territories, the effects of testosterone upon aggression are less clear. In the Blue Tit, *Parus caeruleus*, testosterone implants had no effect on levels of aggression or mate guarding but their offspring were larger and heavier (Foerster & Kempenaers 2005). Where females aggressively compete for males, testosterone also increases agonistic displays and acts in some vertebrate species (e.g. testosterone implants in lizards, *Anolis carolinensis*, Woodley & Moore 1999; Syrian Hamsters, *Mesocricetus auratus*, Faruzzi *et al.* 2005). The female hormones, oestradiol and progesterone, are also correlated with female aggression usually with higher levels of these hormones seen in winners of fights (Rubenstein & Wikelski 2005), although the mechanism is unknown.

Stress hormones (corticosteroids and glucocorticoids) have often been measured during and after contests as these are involved in the flight or fight response and are thought to physiologically prepare the individual for action. In mammalian vertebrates and avian cooperative breeders, dominance is often associated with high glucocorticoids and it has been suggested that the effort of exerting dominance as well as defending sites or engaging in reproductive behaviour results in high stress levels (Creel 2005). In nonmammalian vertebrates, the converse is true with winners having lower stress hormone levels compared with losers. Selective breeding for stress responsiveness has produced two lines of Rainbow Trout, *Oncorhynchus mykiss*, which show low or high cortisol release in response to a stressor (Pottinger & Carrick 2001). In pairwise fights between these lines, low stress responsive individuals are always dominant over high stress responders but it is not known whether this link between cortisol and aggression is causal or consequential. Social isolation of Swordtails, *Xiphophorus helleri*, results in significant reductions in both testosterone and corticosteroids correlated with reduced aggressiveness (Hannes & Franck 1983). Therefore, stress responsiveness or regulation of hormone release may give an individual an advantage when engaging in fights thereby improving social status and access to mates.

Rapid changes in neurohormones also affect aggressive behaviour in agonistic contests. Biogenic amines or catecholamines such as serotonin and dopamine have been shown to differ between winners and losers

in various species. Low serotonin concentrations taken *in vivo* from the cerebrospinal fluid of free ranging Rhesus Monkeys, *Cercopithecus aethiops sabaesus*, are correlated with high dominance rank (Higley *et al.* 1992). Defeats also result in higher serotonergic activity in the brain of Rainbow Trout with winners having a much lower activity (Overli, Harris & Winberg 1999).

Very little is known with regards to invertebrate stress or sex hormones and their impact upon agonistic behaviour possibly due to the fact their endocrinology is very different from vertebrates but studies have investigated the neurohormones. Crustacean models have yielded important insights into the mechanisms of serotonin and aggression (Kravitz 2000). Unlike vertebrates, high serotonin levels are found in winners of fights in shore crabs, *C. maenas* (Sneddon *et al.* 2000b), and crayfish, *Orconectes rusticus* (Edwards & Kravitz 1997). After defeat, serotonin inhibits neurons, whereas it is excitatory in winners in the crayfish (Kravitz 2000). Other amines such as low dopamine in winners of shore crab fights and increased octopamine in winners of field cricket contests (Adamo, Linn & Hoy 1995) show dramatic fluctuations from pre-fight levels to those after contests. Indeed in shore crabs, winners had higher levels of serotonin before fighting and perhaps relative concentrations of serotonin could be used as a predictor of fight outcome (Sneddon *et al.* 2000b). Thus investment in physiological or hormonal status would also be desirable to ensure a competitive edge and in the breeding season these hormones levels are crucial in male success when fighting over females.

Physiological constraints and theoretical models of fighting

The idea that fighting can be costly has been central to theoretical studies of contest behaviour since the early 'Hawk-Dove' models of the 1970s through to the most recent developments. Empirical evidence shows that much of the cost results from proximate physiological changes that occur due to fighting; both hormone and metabolite levels have been shown to constrain fight intensity and influence strategic decisions. However, the fact that fighting is costly does not automatically mean that these costs are sufficiently high to constrain agonistic performance and this may only occur when contests are particularly prolonged or intense. In low intensity contests 'circumstantial' costs – those that accrue as a result of time lost to other activities or factors such as elevated predation risk – may have a more important role. Although both circumstantial and physiological costs will accumulate during the course of a contest, due to their fundamentally different natures they may do so at different rates. Current models do not take into account the fact that the costs of fighting may come from different sources and that the relative importance of the different costs may vary between contests with factors that determine contest

intensity, for example the degree of asymmetry in RHP or in the motivation of each opponent.

Physiological costs have been thought of as 'proximate' costs of fighting and it is implicit in the theoretical models that the energetic costs have an immediate effect on the behaviour of fighting animals. For example, the EWOA model assumes that the rate of cost accrual should determine changes in the intensity of agonistic signals during the contest. Thus, if the costs accrue sublinearly escalation is possible but if there is a greater than linear rate then this will act as an immediate constraint causing de-escalation in intensity. Accumulation of lactic acid appears to be an important cost across a variety of taxa. In some cases (e.g. Hermit Crabs) this does appear to constrain the use of agonistic signals within the time-scale of the contest but in other examples (e.g. velvet swimming crabs) there is no evidence for this. In this example it appears that the 'cost' of accumulated lactic acid – an oxygen debt – is paid after the contest in the form of reduced activity rates. A second direction in which theoretical models could be developed is therefore to account for variation in the timing of when costs that accrue during fights have their strongest effect on behaviour.

A third finding from empirical studies of the physiological consequences of fighting is that different roles adopted during contests may be subject to different costs and constraints. In Hermit Crabs, for example, attackers but not defenders give up when their lactate is high and the decisions of defenders are more strongly influenced by available energy reserves than are the decisions made by attackers (Briffa & Elwood 2005). Many contests, particularly those where one individual holds a resource that its opponent attempts to prise away, involve two distinct roles that use different agonistic behaviours and may therefore be subject to different types and magnitude of cost.

Finally, it is increasingly clear that causal links between physiological status and fighting performance may act in both directions, such that behavioural decisions may be a cause as well as an effect of physiological change. This situation is paralleled in the work on both energetics and hormones. In cichlids, for example, dominance status will influence aggressive ability, but engaging in a contest will cause changes in the levels of the same hormones that influence dominance status. Rapid changes in hormonal status during fights may be vital in understanding motivation since if pre-fight levels are higher in one individual and relative hormone levels decide the victor of a contest, this individual may be physiologically fitter. Endocrine control of the development of male traits and the hormonal control of aggressive behaviour is still poorly understood but research in this area is vital to understand how physiology underlies sexual and natural selection.

Theoretical studies have taken into account the fact that contests may be 'asymmetric' in terms of fighting ability, information and motivation but studies of the physiology of fighting show that there are further

asymmetries relating to the costs of engaging in agonistic encounters: (1) in the balance of intrinsic and circumstantial costs; (2) in the timing of when the costs exert their maximal effect on behaviour; (3) in the nature of the costs that accrue to different roles; and (4) in the causal relationship between physiological costs and changes in behaviour. Incorporating these factors into theoretical studies of contests behaviour may give further insights into how the proximate costs of fighting may act as constraints, by limiting the intensity of agonistic behaviour and influencing the strategic decisions that fighting animals make.

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