Animal Contests

Contests are an important aspect of the lives of diverse animals, from sea anemones competing for space on a rocky shore to male ibex contending for access to females. Why do animals fight? What determines when fights stop and which contestant wins? Addressing fundamental questions on contest behaviour, this volume presents theoretical and empirical perspectives across a range of species.

The historical development of contest research, the evolutionary theory of both dyadic and multiparty contests and approaches to experimental design and data analysis are discussed in the first few chapters. These topics are followed by reviews of research in key animal taxa, from the use of aerial displays and assessment rules in butterflies and the developmental biology of weapons in beetles, through to interstate warfare in humans. The final chapter considers future directions and applications of contest research, making this a comprehensive resource for both graduate students and researchers in the field.

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To Lidia, Fenna and Zenta
and to Kate, Ben and Fergus

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Foreword
A personal history of the development of animal contest theory and its role in the 1970s

Geoff A. Parker

This book on *Animal Contests* represents a landmark in evolutionary biology that is greater than its immediate title suggests. The adaptive interpretation of fighting behaviour in animals has been a catalyst in the study of evolutionary adaptation: first, it was influential in changing concepts about the mechanism of selection (from implicit group selection to individual selection), and second, it was the focus for shaping our understanding of frequency-dependent optimisation in biology through the evolutionarily stable strategy (ESS) approach. I regard it a great privilege and honour to have been invited by the Editors to write a Foreword, and I would like to use this opportunity to recount some of the history of these roles of contest theory in evolutionary biology, including my personal recollections of the events during that very exciting decade, the 1970s.

Before 1970

The way we now think of animal fighting behaviour owes most to the development of the first theoretical models of animal contests, developed in the 1970s. Before this time, with a few notable exceptions (e.g. Williams 1966, Lack 1968), most researchers in the disciplines of ethology and ecology routinely (and usually implicitly) applied group or species selection interpretations to what they saw. This ethos did not generally apply to evolutionary biologists or population geneticists, whose analyses were usually founded on principles derived from Darwinian natural selection. Fighting or threat behaviour in animals is common, especially male–male combat (interpreted in the context of sexual selection by Darwin 1871), but also in food-fighting, territoriality, social dominance, and in various other contexts, and sometimes in both sexes. It can generally be related to contest competition for some limited, unsharable, fitness-related resource, although this is not always immediately obvious.

Although male–male combat aspects of sexual selection had many followers after Darwin's (1871) treatise and even up to half a century later (e.g. Richards 1927), the influential reviews of Huxley (1938*a*,*b*) had been sceptical about female choice aspects of sexual selection, and unenthusiastic even for male–male combat over females, favouring indirect interpretations based on natural selection. An era followed in which sexual selection was largely ignored. This coincided with the 'advantage to the species' culture that gripped ethology and ecology until the 1970s, broken only by Bateman's (1948) classic sexual selection paper. The prevailing ethological view of contests related essentially that contests had evolved into ritualised threat displays to prevent serious injury (Chapter 2).

This philosophy pervaded the literature for over three decades. For example, Leuthold (1966), in his field observations of the Uganda kob, *Adenota kob thomasi*, concluded that territorial breeding grounds offer ecological advantages, such as providing a social organisation and a spacing mechanism to the population and ensuring maximum efficiency of reproduction. Similarly, Norman Moore, rightly recognised as a distinguished dragonfly researcher, clearly avoided intra-sexual selection as an interpretation of the territorial fighting of male dragonflies. He suggested instead that territorial behaviour had a selective advantage related to 'dispersal of the population' (Moore 1952), and went on to list six functions of male–male fighting: colonisation of new breeding areas, prevention of interference with sexual behaviour, prevention of interference with oviposition, prevention of food shortage, reduction of losses to predators, and reduction of time spent in aggression (Moore 1957). He later refined this further, concluding that territorial behaviour is of selective advantage in helping to maintain the most viable stock in the most suitable habitats, reducing disturbance of mating and oviposition and unnecessary fighting, and causing dispersal of sexually mature males to new habitats (Moore 1964). Although implicit species-advantage interpretations of male territorial guarding were generally then the rule, there were some very notable exceptions; Merle Jacobs' (1955) beautiful work deserves special credit for throughout interpreting dragonfly fighting, mate-guarding and territoriality in terms of individual benefits through intra-sexual selection. Moore cited Jacobs' study, but avoided any mention of sexual selection. This instance gives some indication of the unpopularity of sexual selection and obvious individual-advantage explanations before the 1970s, even for male–male contests at leks.

In most research communities there was thus a curious lack of communication between ethologists/ecologists and evolutionary biologists/population geneticists, which became evident in the group selection debate, beginning in the 1960s with Wynne-Edward's (1962) treatise and *Nature* paper (1963) promoting group selection, and its rejoinders (Maynard Smith 1964, Perrins 1964, Williams 1966). Wynne-Edwards, a field ecologist, interpreted territorial fighting as an adaptive mechanism preventing over-exploitation of resources by a population but, with clarity of vision rare for mainstream ecologists of that time, he realised that such a function ran counter to Darwinian natural selection and proposed an alternative mechanism ('inter-group selection') to account for its evolution. Controversy over the relative importance of group and individual selection continues to this day.

Numerous studies before the 1970s had described fighting behaviour and noted the prevalence of settlements by 'threat displays' without damaging combat; many researchers, including such notable ethologists as Lorenz and Huxley (Chapter 2), stressed the evolution of 'ritualistic display' as a means of avoiding dangerous aggression leading to severe injury, with implicit species-advantage benefits. However, not all researchers adhered to this orthodoxy, and individual-selection interpretations of combat behaviour existed if sought for. For example, Valerius Geist, a field ethologist with extensive experience of ungulate behaviour, reviewed observations of fighting involving weaponry such as horns and tusks, which suggested that when combatants can injure opponents, they do so (Geist 1966). He perceptively concluded that contests could be seen as the interplay between defensive and offensive behaviour:

> . . . horns evolved to function as weapons inflicting damage; as defense organs shielding their owner; as binding organs allowing opponents a secure lock in battle; as display organs having an a priori intimidating effect on certain conspecifics.

This individual-selection interpretation of an arms race between attack and defence still appears valid.

The behavioural ecology revolution

Although the seeds were sown in the 1960s, the 1970s hailed a remarkable renaissance in the study of behavioural adaptation: the 'behavioural ecology revolution' (Parker 2006). It marked a paradigm shift in the way that most ethologists and ecologists interpreted the adaptive value of behaviour. After the long era of group/species selection, behavioural adaptations began to be interpreted differently, as characterised by three features: (i) replacement of the 'survival value to the species' shorthand with adaptive explanations based on advantage to the individual (Williams 1966), (ii) the understanding that the evolutionary interests of interacting individuals could be in conflict, and (iii) the introduction of optimality approaches, including the evolutionarily stable strategy (ESS) approach (Maynard Smith & Price 1973), to predict expected behavioural strategies.

These changes were to revolutionise our understanding of animal behaviour. In particular, they changed completely how we now think about animal contests. The key early contest theory papers are summarised in Table A, and their numbers in the Table are given in the text below, beginning with Maynard Smith & Price's seminal work [1].

Assessment strategy and RHP

My own interest in animal contests began at the University of Bristol while watching the mating behaviour of dung flies, *Scatophaga* (= *Scathophaga*) *stercoraria* L., beginning as an undergraduate final-year project in spring 1965, and later my PhD project, 1965–1968 (Parker 2001, 2006, 2010). In these ubiquitous flies the sexes meet around fresh cattle droppings, the site of mating and oviposition. Males paired

Table A Key animal contest theory publications of the 1970s.

No.	Publication	Receipt, revision and publication dates (where known)	Summary of key elements	Google Scholar citations (17.05.12)
1	Maynard Smith & Price (*Nature*, 246, 15–18)	*Published:* 2 Nov 1973	Introduction of the ESS concept, symmetric Hawk–Dove (= 'Mouse') games with discrete injury costs, showing that an ESS can involve limited escalation. Presented solution for the symmetric war of attrition.	2917
2	Maynard Smith (*Journal of Theoretical Biology*, 47, 209–221)	*Received:* 10 Jan 1974 *Published:* September 1974	Development of ESS concept and full derivation of symmetric war of attrition. First analysis of a game with an 'arbitrary asymmetry' (i.e. not affecting potential gains or contest costs) between two otherwise identical opponents, showing that this can be used as a 'conventional settlement.	1420
3	Parker (*Journal of Theoretical Biology*, 47, 223–243)	*Received:* 18 March 1974 *Published:* September 1974	First investigation of payoff relevant asymmetries between contestants in resource value and 'resource holding power (or potential)' or RHP. Analysis was not formally ESS, but best strategy depended on opponent's best strategy. The proposed 'assessor rule' (see text) was later shown to be an ESS (Hammerstein & Parker 1982).	1097
4	Maynard Smith & Parker (*Animal Behaviour*, 24, 159–175)	*Received:* 8 May 1975 *Revised:* 26 June 1975 *Published:* February 1976	Introduction of symmetric 'Hawks–Doves' game; first ESS analysis of payoff relevant asymmetries (i.e. resource value and RHP), definitions of 'commonsense' and 'paradoxical' strategies, and simulations of a game in which information about RHP is acquired during the contest.	1126
5	Parker (In: *Sexual Selection and Reproductive Competition in Insects*)	*Received:* early Feb 1977 *Published:* April 1979	First formal analyses of inter-locus sexual conflict, an asymmetric game between males and females, and parameter space over which it can occur in various contexts. Simulations of asymmetric war of attrition and asymmetric opponent independent costs game (an arms race game).	802
6	Maynard Smith (*Evolution and the Theory of Games*)	*Preface date:* Nov 1981 *Published:* 1982	Maynard Smith's monograph on ESS, reviewing contest theory and many other areas to which ESS theory can be applied.	7183

to females are attacked continually by the many single males searching for females on and around droppings; should a male's elaborate defences fail, an intense struggle ensues between the two (or more) males (Parker 1970*a*). If a 'take-over' occurs, the new male mates immediately with the female. The fights are impressive, and appear to be costly, not only to the male combatants but also to the female they are competing for. The biologist and novelist Robin Baker and I were fellow students at Bristol during our undergraduate and postgraduate years. During our final year as undergraduates we often discussed the mechanism of selection, and as a result – I like to think to our credit – we became individual selectionists, despite the prevailing culture in ecology and ethology.

My PhD field study of sexual selection and mating behaviour in dung flies caused me to be fascinated by the problem of the evolution of animal contests. I could see that fights were costly, and I liked the Lorenzian idea that individuals fight to gain some resource that increases fitness. I could also see that from an individual selection perspective, self's best strategy depended on the opponent's strategy and on the differences between self and the opponent, and that these features must shape the behaviour we observe in animal fights. It was something I had often talked to

Robin Baker about at Bristol, but I did not start work on this problem until around 1970, a year or so after beginning a lectureship at the University of Liverpool. By mid 1973 I had done much of the work for a theory paper that was published in 1974 [3]. I suggested that the opponents in a contest should respond to (i) asymmetries in the value of the resource to each opponent (I called these resource values 'payoff asymmetries' or 'fitness budgets for fighting') and to (ii) asymmetries in their 'resource holding power' (RHP, which changed later to 'resource holding potential' [4]), a measure of a given opponent's absolute ability to defend the contested resource. I used the term RHP rather than fighting ability directly, because the ability to hold or gain the contested resource and to avoid or to inflict contest costs depended on a suite of aspects: e.g. condition, size, strength, weaponry, position and experience.

My basic idea was that if opponents can assess these asymmetries perfectly, and costs rise continuously during an escalated fight, the contest should be settled conventionally without costly escalation, using the following 'assessor rule' (abbreviated for clarity):

> . . . disputes should be decided by each individual's fitness budget available for expenditure during a fight . . . and on the rate of expenditure of the fitness budget if escalation occurs (determined by the RHPs of the combatants) . . . strategies ('assessments') will be determined by . . . which opponent is likely to expend its fitness budget first, should escalation occur. This 'loser' should retreat (before escalation) and the winner should stay in possession of the resource.

To state this rule formally for constant cost rate expenditure, suppose that opponents A and B have resource values V_A and V_B, respectively (V is a measure of benefits of winning, i.e. how much A or B's fitness increases by winning outright, without costs). Should an escalated contest occur, fitness costs increase at constant rates, c_A to A and c_B to B. The assessor rule is that B should retreat immediately without contesting if it assesses that $V_A/c_A > V_B/c_B$. My intuitive reasoning was that A could still achieve a positive gain from the contest after the time that B would sustain a loss from further fighting even if B were to win. I had certainly not proved that this would be an ESS (Maynard Smith and Price's key paper [1] had not been published at the time I was doing this work; see below), although the assessor rule is indeed an ESS if opponents make rare mistakes in assessment of roles A and B, with roles defined as $V_A/c_A > V_B/c_B$ (Hammerstein & Parker 1982, see below).

If assessment is perfect, why should we ever see escalation? I argued that in escalated combats, opponents might sustain damaging injuries rather than continuous costs. The contest could be seen as a series of bouts in which the initial RHP differences between opponents gave an estimate of the probability that the opponent with lower RHP would sustain the injury (the probability that A wins is $RHP_A/(RHP_A + RHP_B)$). The loser sustains an injury that reduces its RHP, which could then affect its decision to continue the contest. I constructed quite a complex model in which there was a normal distribution of RHP in the population of contestants; the highest RHP individuals held a fixed proportion of the resources and individuals with randomly assigned RHP held the remainder. This enabled calculation of the expected search costs incurred in finding an alternative resource (decreasing as an individual's RHP increases), and hence (given a fixed cost of injury to one opponent) what would be the best strategy for each opponent – to persist (if a positive future expectation) or to retreat (if negative future prospects). By simplifying this to a one-round contest, I concluded that

> . . . there should be an escalation range of closely matched combatants and that on either side of the range for a given individual, the higher ranking opponent should usually be prepared to escalate and the lower one to withdraw. Much fighting follows this pattern.

This seemed an intuitively satisfying conclusion, and one that has been supported by more recent game-theory models in which information about RHP is acquired during successive bouts in a contest (e.g. the 'sequential assessment game': Enquist & Leimar 1983).

The birth of the ESS

Little did I realise that at the same time as I was working on my 1974 paper [3] John Maynard Smith and George Price were formulating the seminal concept of ESS, and specifically, had been stimulated to derive ESS logic in order to interpret animal contests [1]. I first heard of this from the population geneticist, Brian Charlesworth, then at Liverpool, when mentioning my work on the evolution of fighting behaviour to him in late 1973. I cannot pretend to have been delighted by this news; my paper was already in early draft stages and I had invested much time on it. Little did any of us realise how much Maynard Smith and Price were to change modelling in evolutionary biology and our own work in the future.

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The American George Price was a remarkable, tragic genius whose religious convictions drove him to share his home and possessions with the homeless; a venture that ended in his suicide in 1975, aged 52. His poignant story is the subject of an acclaimed monograph by Harman (2010) and a fascinating essay by Schwartz (2000). John Maynard Smith was also a remarkable person (obituary by Charlesworth & Harvey 2005): a major figure, liked and admired by several generations of scientists, and greatly revered for his fundamental insights, his incisive and clear-thinking approaches, and for his help and friendship to young researchers. Price had written a manuscript on contests for *Nature*, proposing that animals had been selected not to escalate in fights as a result of selection on individuals, to avoid receiving damage through retaliation by their opponent. It was written as a rebuttal of the ethological notion that animals do not escalate dangerously in contests for the good of the species. Maynard Smith refereed Price's paper for *Nature*, and was stimulated to formalise the concept of the ESS, which Price had alluded to verbally. Price's original manuscript remained unpublished, but eventually, their joint *Nature* publication appeared in late 1973 [1]. The delays involved resulted in the *Nature* paper being preceded by a similar publication in a collection of essays by Maynard Smith (1972).

This key paper [1] concerned models of 'symmetric contests' (i.e. between identical opponents), and besides introducing the ESS concept, it produced two key results for animal contests. First, using simulations with five strategies ranging from 'total war' to 'limited war', and assuming that escalated combat results in costly injury to one opponent, which then concedes victory, they generated a payoff matrix and deduced that 'limited war' strategies could be an ESS. This formed the basis of the 'hawk–dove' type model (Price's religious sensitivities resulted in 'dove' being replaced by 'mouse'). Second, in a model (later called the 'war of attrition' [4]) that assumed that contest costs increased continuously at a constant rate with time, and strategies consisted of a choice of how long to persist in the contest, they showed that no pure strategy (here a unique persistence time) could be an ESS. The ESS was instead a mixed strategy in which each opponent 'chooses' a time t randomly from the probability distribution $p(t) = (c/V)e^{-ct/V}$, where c is the rate of expenditure of costs and V the resource value (mathematical details of these early models are reviewed in Chapter 2).

It is interesting that Geist (1974) criticised Maynard Smith and Price [1] on the grounds that

> It perpetuates the old ethological myth that animals fight so as not to injure each other, or refuse to strike 'foul blows' and, presumably, kill each other ... They were not aware of the published field studies primarily of large mammals which have shown not only how dangerous combat is, but, more importantly, have also led to new theories of explaining aggressive behaviour on the basis of individual selection.

The new theories related mainly to Geist's offence and defence ideas (1966, 1971), which are not incompatible with game-theoretic approaches, particularly those involving sequential assessment and information acquired in asymmetric contests.

ESS and asymmetric contests

I was struck by the fact that Maynard Smith and Price [1] had ignored asymmetries between opponents; they had assumed opponents to be exactly identical except for their fighting strategies. Therefore I thought that my RHP assessment manuscript [3] still had some value, and the fact that it was based on individual selection principles, and seemed at least not incompatible with the new ESS concept, was some consolation. Rather uncomfortably, I had to modify my Introduction to cover the 1973 ESS paper [1] before I submitted my manuscript in early 1974 to *Journal of Theoretical Biology*. I did not know then that a new Maynard Smith paper [2] was already in press in the same journal. Among other things, this paper [2] dealt with 'arbitrary' (or 'uncorrelated') asymmetries – in which the opponents were exactly identical except for some arbitrary 'label' uncorrelated with RHP or resource value, known to both opponents. It showed that an ESS could consist of a 'conventional settlement' in which one opponent gives up without escalation in response to the arbitrary asymmetry, which could be 'prior resident' and 'interloper', while the other is prepared to escalate. Like Valerius Geist, my interest in contests had been stimulated by watching animals in nature; the notion of opponents equal in RHP and resource value was hard for me to accept in reality. John Maynard Smith was a reviewer of my paper [3]; his review suggested some corrections and additions, and broke the news of the new paper that he had in press [2], also in *Journal of Theoretical Biology*. He kindly sent me a copy of the manuscript, so I made additions to cover it and his various reviewer's suggestions, and also those of the other reviewer (possibly

Robert Hinde). Both recommended acceptance, and John's paper [2] and mine [3] were published back to back in 1974.

After reviewing my RHP paper, John invited me to Sussex for discussions, including an overnight stay at his home in Lewis with himself and his wife, Sheila. He was exceptional for his generous encouragement of young scientists, and I quickly came to admire and respect him greatly, both as a person and as a scientist and thinker. Indeed, he has probably been the scientist I have most admired over the three decades we knew each other; he was witty, amiable, immensely stimulating and great fun. His clear, incisive vision and friendly, good-humoured debate (at its best while relaxing with a glass of whisky) have been very much missed since his death in 2004 by all who knew him; it has been one of life's greatest privileges to have known and worked with him. I am acutely aware, with sadness, that it is he who should be writing this Foreword, not me.

We discussed whether an asymmetry such as prior resident/interloper could be respected in a 'conventional settlement' for cases where the retreating opponent had higher RHP and/or higher resource value than the winner, something we later called a 'paradoxical ESS', as opposed to a 'commonsense ESS' in which the winner has higher RHP and/or resource value. This stimulated a collaboration [4], mainly by post. I would pore over John's letters and the algebra they contained, all handwritten, making desperate attempts to work through the maths and to contribute ideas. However, this was indeed an asymmetric contest, and despite his amiable and genial nature, I felt awestruck by John's intellect. At Sussex I had discussed the fact that male dung fly numbers at a dropping show an ESS distribution such that all males (whatever the length of time they stay) gain an equal payoff rate (Parker 1970*b*). This was similar to the prediction for the symmetric war of attrition, and we thought that although it was an *n*-player game rather than a dyadic contest, it had similarities and resulted in a mixed ESS (however, the central reason why male dung flies depart at different times in an ESS fashion is that they show 'input matching' of the female arrival rate; Parker and Stuart 1976). For some reason I cannot remember, possibly due to a reviewer's comment, 'power' in RHP became changed to 'potential'. We went on to show that in a population where opponents have equal RHP but different resource values, and which starts by ignoring asymmetries and playing the symmetric war of attrition based on the mean resource value, only the commonsense ESS would evolve. Analysis of a simple hawk–dove type contest in which opponents have equal resource values but different RHP (and hence probability of being injured) showed that both paradoxical and commonsense strategies could be ESSs, but if there was imperfect information, the commonsense ESS was more likely, having a larger 'zone of attraction'. My main input to our paper [4] was really only to propose certain analyses relating to the probability of evolution of commonsense and paradoxical ESSs, and the 'information acquired during a contest' model, which had some similarities with the model in the second half of my RHP paper [3]. John approached this with a simple computer simulation. Our joint paper on asymmetric contests [4] became an ISI citation classic in 1989.

I had been preoccupied in my 1974 paper [4] by the fact that territory owners usually win against intruders; this issue took up the first half of the paper. I attempted to explain this in terms of the fact that the owner either had more to gain by winning (e.g. a fixed investment must be paid before resources can be extracted from territories) or had higher RHP (e.g. owners represent the truncated top RHP fraction of the population); they were thus commonsense solutions. However, as a result of our collaboration [4], paradoxical conventions also appeared to be a formal possibility, as did conventions based on an arbitrary asymmetry, such as an owner/intruder asymmetry uncorrelated with payoffs or RHP.

These early theoretical models [1–4, Table A] quickly spawned empirical studies that were interpreted within the new framework. Nick Davies's (1978) beautiful study of territoriality in male speckled wood butterflies, *Pararge aegeria* (Chapter 7), was the first and most notable example. Males meet females in small sunlit areas in woodland, and quickly settle in vacant 'sunspots'. However, if a sunspot is already occupied, any intruding male is quickly expelled by the owner. In a clever experiment, in which a series of two males were both duped into 'thinking' they were owners, Davies showed that there was a dramatic escalation in the contest duration, a result which fits with the theoretical prediction that the arbitrary asymmetry of prior residence in a sunspot is used to settle contests conventionally because of the risk of dangerous escalation if the convention is broken. Although prior residence in sunspots may not be an entirely uncorrelated asymmetry (Austad *et al*. 1979, Stutt & Willmer 1998, but see Davies 1979), Davies' study nevertheless fits the predictions for conventions in asymmetric contests, and was highly influential in stimulating a combination of empirical and theoretical approaches.

In 1975–1976, I became fascinated by the theoretical problem of sexual conflict, i.e. evolutionary conflict of interest between males and females, which could be manifest as behavioural conflict in a specific form of asymmetric contest. After convincing myself that there could indeed be evolutionary conflict (despite the fact the male and female having progeny in common), I wanted to know how this conflict might be resolved. For cases where males provide no parental investment other than sperm, I argued that there would be many instances in which, when a male meets a female, it would pay the male to mate but not the female. I made a computer simulation of an asymmetric ('sexual') war of attrition using six discrete time strategies, in which the male persisted and the female resisted. The result, regardless of starting frequencies of the strategies, was 'conventional'; one sex would give up with minimal time cost while the other would retain the strategies for much longer contests (which sex gave up quickly depended on the conditions). I then went on to examine an asymmetric arms race (the 'opponent-independent costs game') a variant of the war of attrition in which the opponent with the higher armament wins. In the war of attrition, the costs felt by each opponent are determined by the persistence time of the opponent with the lower time bid, while here, costs are developmental, and are felt independently by each opponent in accordance with their own 'bid'; they represent costs paid for armament rather than time in a contest. I could not get this simulation to generate a stable solution; instead, the strategies appeared to change continuously (what I called an 'unresolvable evolutionary chase'). This work, which had been a couple of years in gestation, was submitted as a book chapter [5] early in 1977, and was eventually published in 1979. The long delay in press caused me much angst (see Parker 2010, p. 445). At one of the first conferences on evolutionary game theory (in Bielefeld in late 1978), the game-theorist Reinhardt Selten (later to become a Nobel laureate) pointed out that this game could give a stable solution if opponents made small random deviations in strategy (armament) around their mean level; this related to his classic paper (Selten 1975) in which opponents make slight mistakes causing them to deviate from rationality (now called the 'trembling hand' principle). It struck me that the obvious reason for such random deviations in arms level would be random environmental variation, something I later investigated generally for asymmetric arms races (Parker 1983). This was to be my last work on dyadic contest theory, although I have subsequently worked on various types of biological scramble (*n*-player games in which gains from a resource can be shared in proportion to the relative effort of each given competitor, e.g. Parker 2000). But I fear it is true (as the distinguished ecological geneticist, Philip Sheppard, told me early in my academic career at Liverpool University) that one's most important contributions are made by the age of 35 and after then it becomes a matter of refinement. I have included this paper [5] in Table A because it has had more impact in contests in sexual conflict theory (Arnqvist & Rowe 2005) than in animal contests in general.

I have outlined the social history of these early papers of the 1970s at some length, probably partly through sheer nostalgia, although I hope more because of their historic significance: it was a remarkably exciting era (Parker 2006, 2010).

The immediate aftermath

Very soon, a series of theoretical developments followed. For example, the assumption of constant cost expenditure rates in the war of attrition was replaced by non-linear cost functions (Norman *et al.* 1977), followed by much more complex versions allowing general cost and reward functions, and discontinuities and gaps in strategy (Bishop & Cannings 1978, Bishop *et al.* 1978).

The hawk–dove model also received early attention. Treisman (1977) was one of the first to consider fights between relatives (see also Grafen 1979). Hammerstein (1981) examined how perfect information about all asymmetries can permit either payoff-irrelevant asymmetries or payoff-relevant asymmetries to be used conventionally. Under hawk–dove rules, i.e. where the contest ends in a costly injury to one opponent, he clarified that the conventional winning role need not necessarily be the role favoured with respect to payoffs, provided the cost of injury is sufficiently high.

However, a collaboration with Dan Rubenstein in 1978–1979 (during a year I spent at King's College Research Centre, Cambridge) led to the proposal that paradoxical conventions could not hold under war of attrition rules, and that the winning role must always be the one favoured with respect to payoffs (Parker & Rubenstein 1981). In a collaboration with an interesting history (Parker 2010, pp. 450–451), Peter Hammerstein and I confirmed this proposal by showing that in an asymmetric war of attrition, when opponents can make (rare) mistakes about role, only one of two roles can be a winning role, in the sense that the contestant in that role usually gains the resource (Hammerstein & Parker 1982). This winning role A is always a commonsense ESS defined by the payoff-relevant asymmetries. It follows the assessor rule (Parker 1974): the individual in role A is able to persist longer than the opponent before his contest costs exceed the value of the resource, i.e. it is 'retreat immediately if you assess yourself to be in role B, defined as $V_A/c_A > V_B/c_B$'. The closer this inequality, the more likely the opponents are to make mistakes in their assessments of roles A and B, which results in greater escalation. We suggested that this model could be applied to contests between dissimilar opponents such as males and females involved in sexual conflict contests. Note that we did not mean to imply (Chapter 2) that in such cases opponents made mistakes about whether they were male or female; rather the suggestion was that the 'sex label' was just one of many cues by which the male or female opponent could assess whether they occupied role A or B (Clutton-Brock & Parker 1995).

Dan Rubenstein and I had also analysed another version of the 'information acquired in a contest' model (Parker & Rubenstein 1981). Enquist and Leimar (1983) took the idea of information acquired in a contest much further in their 'sequential assessment game'; their formulation has much greater biological reality than earlier models. Like the asymmetric war of attrition, it also predicts greater escalation when opponents are more closely matched.

In the two decades following this early explosion in interest, there have been many further developments in dyadic contest theory (Chapter 2) and also in *n*-player contests (Chapter 3) and the surge of interest spawned Huntingford and Turner's (1987) seminal monograph on animal conflict. My own interest turned mainly to *n*-player scrambles, either generally (Parker 2000) or in specific contexts, such as parent–offspring conflict (e.g. Parker & Macnair 1979) and sperm allocation (reviewed in Parker & Pizzari 2010). John Maynard Smith retained his interest in contests throughout the rest of his life, sporadically producing further developments. His *magnum opus* (if one can be selected out of many) was his book (Maynard Smith 1982) reviewing ESS theory and posing many new ideas [6]; it still receives huge numbers of citations and although published in 1982, not in the 1970s, is included in Table A for completeness. He became interested in whether biological signals could be uncostly (the 'Philip Sidney game'; Maynard Smith 1991); and afterwards, in the general biology of signalling (his final book was on biological signals; Maynard Smith & Harper 2003).

And beyond

In a history of behavioural ecology (Parker 2006), I now believe that I was wrong to claim:

> Though contest behaviour still attracts both theoretical and detailed empirical research . . . it is now less popular. Its greatest contribution to behavioural ecology probably relates to its role in the development of ESS.

I suspect that this conclusion was influenced not so much because, since the 1970s and early 1980s, I had moved on to other areas of research (contest behaviour always remained an interest), but rather because its importance in the development of the seminal ESS concept and as a catalyst in the groundswell against implicit group-selection made subsequent developments appear less notable. There have been many important theoretical and empirical advances in the past 30 years. Indeed, this book shows that what has actually happened, as with many of the areas in behavioural ecology, is that the topic has matured into a fully fledged subject area in its own right. Its early roles in the group selection debate and the development of ESS in the optimality approach to adaptation do not detract from this – rather, they enhance its status as a new discipline, as this volume surely testifies.

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Preface

Mark Briffa & Ian C.W. Hardy

This book is about the evolution of contest behaviour in animals. It covers both predictive theories for contest evolution and empirical evidence. There are several potential strategies for organising an edited book that collects together a diverse range of study systems and a rich body of theory. One would have been to invite authors to each write a chapter about their favourite concept. For example, there are several alternative theoretical explanations (models) for contestant assessment during agonistic interactions that appear frequently in the contest literature (these are introduced in Chapter 1 and detailed in Chapter 2) and MB, along with several other contributors to this volume, has been especially interested in using a particular study-species to test the key features of these models in order to investigate assessment rules and the possible functions of repeated agonistic signals. In other words, we are all interested in how the loser makes the decision to give up, and could each have contributed a chapter along similar lines, covering the relevant theory as well as detailing our own experiments. It soon became apparent, however, that there was a potential cost associated with this layout: as a result of the tight links between theory and experimental work described above, many authors would have wanted to write about the same concepts, albeit applied to different animals, leading to much conceptual repetition between chapters.

Our alternative, and adopted, strategy for organising this book has been to divide it into two main sections, the first dealing with general theory and the second comprising a series of chapters arranged by taxon (in the somewhat uncomfortably traditional ‘invertebrates to humans’ sequence). The link between the theoretical and empirical sections is a chapter on analysis of contest behaviour data. This includes recent advances in our understanding of the appropriate experimental design and analytical approaches for testing hypotheses about contest behaviour, with the aim of providing practical advice to those engaged in empirical contest research. As we see it, this scheme has two main advantages.

First, all of the theory concerning contests, dyadic (pairwise) and then multi-party, is present in a contiguous narrative. This is something that we feel has been missing from recent expositions of contest behaviour, as illustrated by two recently updated textbooks. In the 4th edition of *An Introduction to Behavioural Ecology* (Davies *et al.* 2012), the foundation stones of contest theory, the Hawk–Dove game (Maynard Smith & Price 1973) and the war of attrition (Maynard Smith & Price 1973, Maynard Smith & Parker 1976) are discussed as part of a chapter on competing for resources, while the sequential assessment model (‘SAM’: Enquist & Leimar 1983) is dealt with in a later chapter on communication. Thus, these important components of contest behaviour appear in different parts of the book. Furthermore, the alternative explanations for repeated agonistic displays comprising the energetic war of attrition (‘EWOA’: Payne & Pagel 1997) and the cumulative assessment model (‘CAM’: Payne 1998), which have gained a great deal of recent support from empirical studies, do not fit easily into this way of organising things. In the second edition of *Principles of Animal Communication* (Bradbury & Vehrencamp 2012), these alternative assessment models are discussed in detail, but the theory surrounding other types of contest – for example, fights that result in fatalities and multi-party ‘battles’ – are outside the book’s scope. In both of these books the choices made for dealing with contest theory suit their purposes (to introduce students to the concept of the evolutionarily stable strategy (ESS), and to discuss the role of agonistic signals, respectively). Here, we have aimed to provide an explanation of the totality of contest theory. The manner in which contest behaviour is often discussed, as an interesting addendum to, or subset of, other areas of behavioural ecology research, is possibly a result of the fact that, as noted above, contest theory intersects with so many other questions. Therefore, we believe that what has been lacking and what will be beneficial is having all of the conceptual issues surrounding contest behaviour dealt with in the same place. Recent attempts have been made to do this for assessment models at least (Arnott & Elwood 2009), sometimes within the settings of empirical papers (Kelly 2005, Stuart-Fox 2006, Briffa 2008), but Chapters 2 and 3 of this volume extend this approach to cover basic game-theory models as well as recent ecogenetic models and attrition laws for multi-party contests.

The second advantage is that this way of organising the book frees up the authors of empirical chapters to concentrate on the research findings of their own study systems. Our aim in this respect was not to in any way divorce the empirical work from its theoretical underpinnings; rather, we wanted to avoid unnecessary repetition of theoretical details that can be best exposited elsewhere, in a contiguous fashion. As far as we are aware this is the first collection of taxon-specific reviews of contest behaviour, although this structure has been implemented before in an edited book on that other 'original' topic in evolutionary game theory, sex ratios (Hardy 2002). In editing this volume we have both been struck by the fact that the choices about which sets of questions to study have very clearly been driven by the biological quirks of each study system. Hermit crabs are excellent for investigating agonistic signals (Chapter 5), beetles are ideal for looking at the development of weaponry (Chapter 9) and encounters between rival ant colonies provide insights into multi-party 'battles' (Chapter 8) and different study systems connect naturally to different areas of biological research beyond contest behaviour *sensu stricto*. Moreover, on reading these taxon-specific chapters we formed the distinct impression that the authors are often motivated as much by a passionate interest in (and detailed knowledge of) their study organisms, as by a desire to solve intriguing behavioural ecology questions. We think that the study of animal contests is all the better for this; we hope that our way of organising the book has allowed the different interconnections to be emphasised and the passions of the authors to shine through and, of course, that readers enjoy these chapters as much as we did.

The most recent previous volume to treat contest behaviour as a subject in its own right was *Animal Conflict* by Huntingford and Turner (1987). In spite (or perhaps because) of the fact that the study of animal contests has initiated so many strands within the field of behavioural ecology, contest behaviour has perhaps come to be viewed in recent years as a slightly niche topic. In particular, contests may have been superseded by, or perhaps subsumed into, the vast amount of interest in sexual selection as a potential driver of animal behaviour. We see this largely as evidence for the importance of contests, rather than as indication of their topical demise (although we were concerned to notice that a recent and large textbook explicitly on *Behavioural Ecology* (Danchin *et al.* 2008) only mentioned animal contests *en passant*, as a subset of sexual selection!). A concise version of an integrated approach to contest behaviour is provided by a dedicated chapter (Briffa & Sneddon 2010) in the recent multi-author volume *Evolutionary Behavioral Ecology* (Westneat & Fox 2010). However, in the present book, we hope to provide a more detailed account of both the historical development of, and the most recent advances in, animal contest research itself. We find a historical perspective to any research field to be immensely valuable; as Terry Pratchett has noted: 'It is important that we know where we come from, because if you do not know where you come from, then you do not know where you are, and if you do not know where you are, then you don't know where you are going. And if you don't know where you're going, you're probably going wrong' (Pratchett 2010, p. 423). The overarching aim of this book is, however, to emphasise that contests are an important aspect of the lives of diverse animals, from sea anemones competing for space on a rocky shore to fallow deer bucks competing for access to females, and are therefore a fascinating and important topic of study in their own right. As our respected colleague, and contributor to this book, Bob Elwood, has put it, 'Contests determine the unequal division of resources and thus drive natural selection to a huge extent' (R.W. Elwood, pers. comm.).

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Nearly every chapter was peer-reviewed by at least one internal referee (an author of another chapter) and at least one external referee: although this book has two editors, from the very start we regarded the refereeing process as a crucial element in its ontogeny for the same reasons that journal papers are peer-reviewed. The exceptions to this reviewing process were our brief 'intros and outros' (Chapters 1 and 16). Both were read through by Geoff Parker and the Introduction was also read by Sophie Mowles. The data analysis chapter (Chapter 4) has been reviewed internally by Sophie Mowles and subjected to the scrutiny of two external referees. For internal refereeing of the remaining core chapters we thank: Tim Batchelor, Ryan Earley, Bob Elwood, Tim Halliday, Darrell Kemp (who reviewed two chapters), Hanna Kokko, Dómhnall Jennings, Martin Gammell, Mike Mesterton-Gibbons, Armin Moczek, Sarah Pryke and Emilie Snell-Rood. For external refereeing of these chapters we thank Gareth Arnott, Thomas Breithaupt, James Cook, Sarah Collins, Duncan Irschick, Robert Jackson, Geoff Parker, Sean Rands, Claudia Rauter, Nick Royle and Christer Wiklund. In addition, Michael Reichert and Sophie Mowles initially provided external reviews of chapters but then subsequently became chapter co-authors. We thank Megan Waddington and Dominic Lewis at Cambridge University Press for patiently letting us get on with things and Pat Backwell, Teresa D. Baird, Ludek Bartoš, Patrick Bergeron, William Clarke, Tanya Detto, Sonia Dourlot, Sophie Mowles, Anthony O'Toole, Joyce Poole, Fabian Rudin, Franck Simonnet, Maria Thacker and Martin Wikelski for supplying photographic material and permissions.

Closer to home, we thank our respective families for putting up with our editorial commitments while all sorts of 'bourgeois' events in family life were occurring (such as moving houses and jobs, having children and *not* having enough holidays with them). Finally, we would like to thank each other. We have worked approximately equally on this book. The book's early conception was ICWH's but it was immediately obvious that it would benefit greatly from being co-edited with MB due to our complementary contest behaviour research experiences: in caricature, ICWH tends to focus on contest *outcomes* and also to link contests to other areas of behavioural ecology and applied biology, often using parasitoid wasps; MB tends to work on behaviours occurring *within* contests and to link these to physiological measures, mainly using crustaceans. This book was a fully joint project from well before the stage of being commissioned. To reflect this approximate equality of input, ICWH is first-named editor of the book as a whole while MB is first author of those chapters contributed to by us both: one might say that one of us has won the bouts while the other has won the contest but, actually, the thing we would most like to thank each other for is that we have managed to co-edit a book largely about agonistic dyadic behaviour without actually engaging in any between ourselves.

I.C.W.H., Sutton Bonington
M.B., Plymouth
July 2012

Abbreviations

ADI	average dominance index
AIC	Akaike Information Criterion
ART	alternative reproductive tactics
ATR	'all-trunk raised'
AVT	arginine vasotocin
BIC	Bayesian information criterion
BSA	behavioural sequence analysis
BSA	bovine serum albumin
CAM	cumulative assessment model
DS	David's score
EFOT	expected future ownership time
ESDA	exploratory sequential data analysis
ESS	evolutionarily stable strategy
EWOA	energetic war of attrition
GEE	generalised estimating equation
GLM	general linear model
GLMM	generalised linear mixed model
GLZ	generalised linear model
I&SI	inconsistencies and strength of inconsistencies
LMM	linear mixed models
MID	militarised interstate dispute
MVT	marginal value theorem
OSR	operational sex ratio
PBT	preferred body temperature
PCD	programmed cell death
PCR	polymerase chain reaction
RDNL	relative difference in nematocyst length
RHP	resource holding power/potential
RPH	relative plasticity hypothesis
RWD	relative weight difference
SAM	sequential assessment model
V	resource value
WOA	wars of attrition