Chapter

1

Introduction to animal contests

Mark Briffa & Ian C.W. Hardy

1.1 Animal contests in nature

Next time you stand on a seashore and look carefully with your 'zoologist's eyes', you may be surprised at the high diversity of animal phyla that are present, even within a single intertidal rock pool. If you are patient and can stay still for a few minutes, another surprise in store is the preponderance of aggressive behaviour demonstrated by the intertidal fauna. Depending on which part of the world your rocky shore is in, you might observe some of the following: male Azorean blennies fighting over the nests that they need in order to attract females; pre-copula pairs of shore crabs with inter-male aggression over the ownership of recently moulted females, as these females are only receptive to sperm during a brief post-moult period; common European hermit crabs *rapping* in an attempt to evict an opponent from its gastropod shell; and, if you really have a lot of time on your hands, you might notice slow-moving sea anemones striking one another with special tentacles called *acrorhagi*, during disputes over space. Of course, aggressive behaviour is not restricted to intertidal marine animals. Take a walk in the woods and you could witness aggression over the ownership of territory; this is one of the reasons why male birds sing, why male butterflies perform many of their aerial displays and why armies of female worker wood ants try to kill individuals from a different colony. These examples illustrate two important points about aggression: first, animals will fight over a range of resources, when the ability to access those resources is a major constraint on fitness. In many cases this involves conflict over access to mates, as in the case of shore crabs. However, other resources such as territory, food and shelter are also contested, and influence the fitness of females as well as males. The second point is that aggressive behaviour is extremely widespread among animal taxa: these examples alone are drawn from three different phyla: chordates, arthropods and cnidarians.

1.2 Defining animal contests

How should we best describe the diverse behaviours that we have so far called 'aggressive'? As with many aspects of behaviour there are 'everyday' words that we might use in a fairly loose way. 'Aggression' works reasonably well for most of the examples given above, denoting a particular type of conflict of interests that is resolved through a direct and discrete interaction between the opposing parties, but aggression is a broad term that seems less appropriate for displays in butterflies (Chapter 7) than for examples that involve some form of escalated encounter, perhaps involving injuries, as in hymenopterans (Chapter 8). Huntingford and Turner (1987) discussed this issue in the preface to *Animal Conflict*, the seminal textbook dealing with aggressive behaviour. They also pointed out that a direct conflict between opponents might involve both *defensive* and *submissive* behaviours as well as *offensive* behaviours, and 'aggression' in its everyday sense does not seem to fit well with defence and submission; for example, in human interstate conflict (Chapter 15), the term 'aggressor' is usually applied to the state that is deemed to have initiated the conflict. Therefore, the term 'agonistic' might be more appropriate: agonistic behaviour is 'a system of behaviour patterns having the common function of adaptation to situations involving physical conflict' (Scott & Fredericson 1951). Agonistic is a useful term but, again, while it encompasses both defence and submission, it seems best applied to examples involving attempts to inflict damage on the opponent, or at least where there is some sort of escalated phase involving physical contact. Huntingford

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and Turner (1987) settled on the term '*Animal Conflict*' as one which is broad enough to encompass various forms of direct interaction that result from a conflict of interests. This broad term, however, might also include other types of conflict, such as conflict over survival of the prey item in a direct interaction between predator and prey. In this book we focus on a subset of interactions where the conflict occurs over the ownership of discrete resource units such as mates, food or shelter, as well as territories or positions in a social hierarchy that determine access to these items. Thus, while the form of these interactions is incredibly diverse, the underlying reason is always the same; essential resources cannot be shared and are unlikely to be available in an unlimited supply, so the best way to secure access to the resource is often to take it (or defend it) from another party. Therefore, in this volume we have chosen to use the term '*Animal Contests*'. We define a contest as *a direct and discrete behavioural interaction that determines the ownership of an indivisible resource unit*. This definition seems broad enough to include the aerial displays of butterflies (Chapter 7), the rutting of red deer (Chapter 14) and fatal fighting in ants (Chapter 8), while being specific enough to exclude other types of conflict of interest, such as scramble competition (over resources that are divisible), conflict between parents and offspring (over parental investment) or predators and prey (over dinner). This is not to say that the other terms should not be used to describe specific types of contest; it might be very appropriate to talk about aggression in shore crabs, agonistic displays in fiddler crabs or even 'fighting' in butterflies, but these terms can be thought of as elements of contest behaviour.

1.3 Animal contests and behavioural ecology

Contest behaviour appears to be a significant feature of the lives of diverse animals but, apart from involving a conflict of interests over the ownership of a resource unit, what do the different examples of contest behaviour all have in common? In terms of underlying mechanisms ('how?'), identifying unifying themes is possible but less than straightforward. Variation in testosterone, for example, influences aggressiveness in fish, birds and mammals, but this steroid is absent in non-vertebrate animals. Similarly, while the energetic demands of aggression can be a limiting factor across taxa, the metabolic pathways involved can be quite different; in vertebrates the energy storage molecule that buffers against ATP (adenosine triphosphate) depletion is creatine phosphate whereas in other animals it is arginine phosphate. It is perhaps easier, then, to identify commonalities in the 'whys' of aggression. Behavioural ecologists will recognise this approach, of focussing on questions about the function of behaviour, which is one of Tinbergen's 'four questions' in biology; the others being causation, development and evolution (Tinbergen 1963, Bolhuis & Verhulst 2009). Indeed, the analysis of contest behaviour has been of consistent interest for behavioural ecologists and the field has been characterised by a continuous and productive interplay between theoretical developments and insights gained from empirical studies. An early pioneer, Geoff Parker (see the Foreword) worked on both aspects, his insights from observations of fighting dung flies (Parker 1970) leading to the development of the study of asymmetric contests and the influence of 'resource holding power' (RHP, also termed 'resource holding potential') and 'resource value' on contest outcomes (Parker 1974, Maynard Smith & Parker 1976). RHP can be defined as 'an individual's ability to obtain or retain a resource during a contest', and may comprise several components, both intrinsic and extrinsic to the individual. Resource value (denoted by *V*, Chapter 2) can be defined as the value that the individual places on obtaining or retaining the resource. *V* may be influenced by a number of attributes of the contested resource and also the same contested resource may have different value to different contestants.

This 'RHP and *V*' tradition has enhanced the study of animal contests and has led to some major landmarks in our understanding of why contest behaviour has evolved. Magnus Enquist and Olaf Leimar derived the hugely influential 'sequential assessment model' (SAM: Enquist & Leimar 1983) and later used cichlid fish as an experimental system for its testing (Enquist *et al.* 1990, Chapter 10). Currently, the SAM (Enquist & Leimar 1983) and two later models, the energetic war of attrition (EWOA: Payne & Pagel 1997) and the cumulative assessment model (CAM: Payne 1998), form a triad of theories about the evolution of contest behaviour that have been the subjects of intense empirical research in recent years (e.g. Stuart-Fox 2006). The reason why these three models have been particularly influential is that (a) they are clearly differentiated by their main assumptions about the functions of agonistic behaviour and (b) they make clear predictions that

Table 1.1 Key features of three influential models that have permeated empirical studies of contest behaviour, particularly since the late 1990s. Each assumes a different 'reason' for the use of repeated agonistic behaviours, which in many cases are non-injurious. These assumptions lead to different predictions about the changes in intensity expected during pairwise contests and about the way the contests are structured, discussed in detail in Chapter 2. They also lead to inferences about the expected correlations between RHP and contest duration, discussed in Chapter 4. Chapter 4 also explores the options for appropriate statistical testing of hypotheses about contest duration, dynamics and structure.

Model	Reason for repeated actions	Giving up decision based on	Duration should correlate primarily with RHP of	Duration could also correlate with RHP of	Contest dynamics and structure
Sequential assessment model, SAM	To reduce sampling error in the opponent's estimate of the performer's RHP	Information about the opponent's RHP	Loser (+) Winner (−)		Contests structured into a series of phases characterised by increasingly intense agonistic behaviours; but within phases agonistic behaviour should be performed at a constant rate
Energetic war of attrition, EWOA	To demonstrate the performer's endurance	A threshold of costs that accrue as a result of the loser's actions	Loser (+)	Winner (+)	Constant, escalating or de-escalating within phases
Cumulative assessment model, CAM	To inflict costs upon the opponent	A threshold of costs that accrue as a result of the loser's actions plus costs that are inflicted on the loser by the actions of the opponent	Loser (+)	Winner (+) or Winner (−)	Constant, escalating or de-escalating within non-injurious phases; escalates within injurious phases

are amenable to experimental testing. (Table 1.1 provides a summary of these assumptions and predictions; Chapter 2 considers these models in more depth and Chapter 4 gives details of statistical and experimental design approaches that can be used to distinguish between them.) Thus the tradition of interplay between theory and empirical work continues in the contest literature.

The three models discussed above continue another tradition in animal contest research in that they may also provide insights that can be applied to other areas of behavioural ecology. The body of theory surrounding contest behaviour has always proved remarkably adaptable and it is worth reflecting here on the influence that this body of theory has had on the wider field of behavioural ecology as a whole. Models of contest behaviour were among the very first to utilise 'game-theoretic' reasoning to understand the evolution of animal function. Following hot on the heels of Hamilton's (1967) 'unbeatable strategy' model of sex ratio evolution, Maynard Smith and Price (1973) applied, for the first time, game theory to animal contests in their Hawk–Dove (or 'Hawk–Mouse') model, which explains the evolution of non-injurious fighting. In classical game theory, one asks 'which strategy from a set of strategies should an individual play against an opponent who may also choose from the set of strategies' (think about a game of rock–paper–scissors between two people, but also think about the cold war and nuclear standoffs between super-powers; the application of contest theory to interstate conflict is discussed in Chapter 15 and an evolutionary 'rock–paper–scissors' game occurs in lizard contests, Chapter 12). In evolutionary game theory, the underlying logic is the same but the emphasis has shifted from attempting to anticipate (using rational forethought) the decisions made by individuals (or other entities such as companies or countries) about what strategy to play, to predicting what strategies should be 'chosen' (or 'favoured' or 'selected') over evolutionary time, with natural selection acting as the optimising agent. Game theory shows that the best thing for a focal individual to do will be determined by what others are doing (and vice versa). Game-theoretical reasoning explains the evolution of behaviours that, if analysed naïvely

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and superficially, might seem to be counter-intuitive results of natural selection (such as using signals to resolve a contest). Rather, evolutionarily stable strategies (ESS) arise because individuals act to maximise their own fitness, and these strategies therefore tend to be at variance with what would benefit the group as a whole. Another key insight was that frequency-dependent selection can lead to the evolution of stable mixes of alternative behavioural strategies. The publication of Hamilton's (1967) and Maynard Smith and Price's (1973) game-theoretic models spawned large and successful literatures within evolutionary and behavioural ecology: for sex ratios, for instance, see Hardy (2002) or West (2009) and for contest behaviour, continue to read this book.

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References

Bolhuis JJ & Verhulst S (eds.) (2009) *Tinbergen's Legacy: Function and Mechanism in Behavioral Biology*. Cambridge: Cambridge University Press.

Enquist M & Leimar O (1983) Evolution of fighting behaviour; Decision rules and assessment of relative strength. *Journal of Theoretical Biology*, 102, 387–410.

Enquist M, Leimar O, Ljunberg T, *et al.* (1990) A test of the sequential assessment game: Fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, 40, 1–14.

Hamilton WD (1967) Extraordinary sex ratios. *Science*, 156, 477–488.

Hardy ICW (ed.) (2002) *Sex Ratios: Concepts and Research Methods*. Cambridge: Cambridge University Press.

Huntingford FA & Turner A (1987) *Animal Conflict*. London: Chapman & Hall.

Maynard Smith J & Parker GR (1976) The logic of asymmetric contests. *Animal Behaviour*, 24, 159–175.

Maynard Smith J & Price GR (1973) The logic of animal conflict. *Nature*, 246, 15–18.

Parker GA (1970) The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). IV. Epigamic recognition and competition between males for the possession of females. *Behaviour*, 37, 113–139.

Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, 47, 223–243.

Payne RJH (1998) Gradually escalating fights and displays: The cumulative assessment model. *Animal Behaviour*, 56, 651–662.

Payne RJH & Pagel M (1997) Why do animals repeat displays? *Animal Behaviour* 54, 109–119.

Scott JP & Fredericson E (1951) The causes of fighting in mice and rats. *Physiological Zoology*, 24, 273–309.

Stuart-Fox D (2006) Testing game theory models: Fighting ability and decision rules in chameleon contests. *Proceedings of the Royal Society of London B*, 273, 1555–1561.

Tinbergen N (1963) On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20, 410–433.

West SA (2009) *Sex Allocation*. Princeton, NJ: Princeton University Press.

Chapter

2

Dyadic contests: modelling fights between two individuals

Hanna Kokko

2.1 Summary

Animal contests were the focal topic that brought game theory to the attention of behavioural ecologists, giving rise to evolutionary game theory. Game theory has remained by far the most popular method of deriving theoretical predictions ever since, although it nowadays coexists with other methods of analysis. Here I review the developments to date and highlight similarities and differences between models. There is a clear progression from simple two-player models with fixed payoffs to explicit tracking of fitness consequences in a population context. In many cases this development has helped to discover that some of the early predictions may have been misleading. Despite the large number of current models, there are still gaps in the theoretical literature: sometimes simplifying assumptions have been relaxed in one context but not another. I hope that by highlighting these gaps theoreticians will be provided with new research ideas, and empiricists will be encouraged not only to distinguish between existing models but to be able to point out assumptions that are essential for deriving a result yet may be violated in existing systems, thus directing new modelling in the most useful direction.

2.2 Introduction

Until the mid 1960s, animal contests were viewed using group selectionist thinking. Julian Huxley (1966) thought that ritualised fights evolved to limit intraspecific damage, partly based on Konrad Lorenz's (1964, 1965) ideas that species need to evolve mechanisms that limit aggression in species that possess dangerous weapons for other reasons, e.g. as adaptations for capturing prey. Following George C. Williams' (1966) book *Adaptation and Natural Selection: A Critique of Some Current Thought*, however, biologists became aware of the need to distinguish between explanations that are based on benefits to the individual versus those that rely on benefits accruing to a group (or a species). This immediately raises the question of what limits aggression in animal populations. There are many instances where individuals interact peacefully, even cooperatively. While the evolution of cooperation is beyond the scope of this chapter, refraining from maximal aggression appears similarly puzzling if one expects selfish genes to be as ruthless as possible. Animal fights can be lethal, but very often they are not. Encounters between neighbouring territory owners, for example, often involve a lot of display and only rarely escalate to physical contact. A 'mutant' that always strikes first and kills a neighbour might be expected to spread, until the orderly territorial system is destroyed in the population. Why does it not? Likewise, male snakes wrestle for mating opportunities, but do not generally use their fangs against each other (Maynard Smith & Price 1973). Why not use all weapons available, given that the loser's genes will not be propagated into the next generation?

These kinds of questions prompted a new wave of animal behaviour studies in the 1970s. These studies made use of an approach derived from mathematical economics: John von Neumann, Oskar Morgenstern and John Nash had developed *game theory* in the early half of the twentieth century. Game-theory models seek best responses of individuals given what other individuals in the group or population are doing; in other words, game theory is about making decisions in the presence of other decision-makers. In the 1970s it was realised that game theory is the ideal tool to study the evolution of behaviour in non-human

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animals as well. Economists had made the assumption that their players are rationally calculating what is best for them, but as natural selection rewards best strategies, no conscious thought is required in evolutionary game theory (even plant growth can be modelled using game-theoretic tools, see Falster & Westoby 2003 for a review).

Many of the early papers that contain game-theoretic treatments of animal contests explicitly mention that this approach offers a novel alternative to earlier group-selectionist thinking (Maynard Smith & Price 1973, Maynard Smith 1974, Parker 1974). In papers published today, this contrast no longer needs to be made. Game theory has established itself as the most important tool for developing theories of dyadic contests, and it peacefully coexists with supporting alternatives such as individual-based simulations (e.g. Kemp 2006, Just *et al.* 2007) and genetic algorithms (Hamblin & Hurd 2007). This chapter will follow this development to date.

The focus of this chapter is on interactions between two individuals. Multi-contestant games are developed in Chapter 3, together with associated topics such as dominance hierarchies and winner–loser effects. Although in principle a dominance hierarchy can form between just two individuals, in practice these topics usually require attention to interactions that happen in larger groups (Crowley 2001). It is also a central theme of the current chapter that the history of dyadic fighting models shows an increasing appreciation of the importance of population-level phenomena, as these can have a strong influence on the traits of the two individuals in question.

2.3 Notation

Contest models have very often differed in notation. While it does not matter whether a non-aggressive individual is said to play ‘Dove’ (Maynard Smith 1982), ‘Careful’ (Crowley 2001, Kokko *et al.* 2006) or ‘Mouse’ (Maynard Smith & Price 1973) if the mathematical essence of the strategy remains the same, wildly varying notation makes it obviously harder to grasp similarities between models. It is fortunate that many models have now converged on roughly similar terminology. In this chapter I freely ‘mistreat’ published models by recasting them using the notation summarised in Table 2.1.

The most important variables, present in many models, are resource value V, cost of fighting C, time t, and the probability p that a specific individual will win a fight. The individuals in question will be labelled as A and B, where A is in the ‘favoured’ role (if there is one; sometimes $p_A = p_B = p$). Often ‘favoured’ means that $p_A > p_B$ if the situation escalates to a fight but, depending on context, the ‘favoured’ role has been used to mean a discoverer of a resource (such as the prior owner of a territory) or an individual with higher Resource Holding Power, or one who would benefit more from possessing a resource. Strategies will be called *commonsense* if they lead to the favoured individual being the more likely one to win, and *paradoxical* in the opposite case. Strategies are called *conventional* if one of the contestants immediately retreats after some asymmetry is observed (although in the literature one also finds ‘conventional’ used roughly synonymously with ‘limited war’, i.e. no immediate escalation to maximal use of weapons, e.g. Maynard Smith & Price 1973). Contrasting with the probability of winning a contest, p, the context-dependent variable P will be used for all other probabilities, such as the relative frequencies of different individuals, or the probability that an individual uses a specific tactic. Resource Holding Power, also called Resource Holding Potential (RHP: Parker 1974), typically does not have a variable name assigned to it, but it is often implicitly present in models such that the cost of fighting is low for an individual with high RHP (e.g. $C_A < C_B$ if A is physically larger, but see section 2.6.2.1. for why this might not always hold). In fights that consist of several bouts, or that have an explicit duration expressed in continuous time, C denotes the total cost accumulated while c

Table 2.1 Commonly used notation. The consensus notation is used in this chapter even if notation in original models differs from this. This list does not include notation that only occurs in specific models (see text).

V	Value of the resource
V_0	Value of future life
c	Rate of cost accumulation
C	Total cost; C^* if denoting the ESS
A	Favoured individual (often because of higher V/C than that of opponent)
B	Disfavoured individual (often because of lower V/C than that of opponent)
p	Probability of winning a fight
P	Generic probability (e.g. frequency of specific type of individuals)
t	Time

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denotes the per-bout cost or rate of cost accumulation in the continuous-time case, respectively.

2.4 A categorisation of models

Dyadic contest models differ in several respects. Obviously, the precise *question* to be asked can differ between models: a model of lethal combat (Enquist & Leimar 1990) will take a different form than an analysis of whether the location of a territorial boundary should be settled based on a landmark (Mesterton-Gibbons & Adams 2003). The majority of models are of a generic 'winner takes all' type (the contested resource is indivisible), where the winner gains a resource of value V and the loser gains nothing (although some models additionally ask whether V is necessarily the same for both players). Of course, 'winner takes all' does not mean that the winner's fitness is large and the loser's is zero. As pointed out by Maynard Smith (1982, p. 11), the loser simply keeps what it otherwise had in life, and if V is small the interpretation may be that the winner got one food item that the loser did not. It is intuitively clear, as well being a prediction of many models, that if V is small compared to the alternative options (which are sometimes denoted by V_0), individuals are not prepared to fight to death (Enquist & Leimar 1990).

There are other important differences between the models. One can distinguish between *black box* and *open box* models. In a black box model, the link from the two strategies to the outcome of the fight is a single step and all further detail is hidden from view. For example, consider the 'Hawk–Dove' game, a classical game with somewhat unfortunate strategy labels (in reality hawks are predators of doves, but the game refers to fights among conspecifics; neither are doves especially benign species). An aggressive 'Hawk' is assumed to beat a non-aggressive 'Dove' and gain V units of fitness, while two 'Hawks' gain the expected value $(V - C)/2$ each (section 2.5.1). In neither case, nor in encounters between two Doves, does the model specify the sequence of events during a fight. All we know is that if two Hawks enter the 'black box', they emerge after a fight and one of them has some form of injury that cost it C fitness units. Mathematically it does not even matter if it is the loser or the winner who suffers the cost C, or if both suffer equally $(C/2)$: both interpretations imply that expected fitness, calculated before the winner is known, is $p(V - C)$ where $p = 1/2$.

Open box models, e.g. the sequential assessment game (Enquist & Leimar 1983), make much more detailed predictions about fight durations, the distribution of costs accumulated before the fight ends, the level of escalation reached by the end of the fight and other similar measures. The level of detail is not a goal in modelling as such: different models exist for different purposes and very simple models are often best for explaining general logical structures, such as the nature of frequency-dependence in contests.

Finally, models differ in whether individuals participating in a contest make use of *information*. The simplest Hawk–Dove games investigated frequency-dependent selection with an implicit assumption that individuals use genetically predetermined levels of aggressiveness and do not modify their behaviour according to the type of opponent encountered. The outcome of the fight, on the other hand, *does* depend on the type of opponent encountered in these models, which is why game theory is used in the first place. Best responses can evolve despite no explicit information-gathering, because evolution itself equips individuals with information about *average* frequencies of Hawks and Doves in the population. Often, however, individuals can do better than to base their decisions on the likely distribution of opponents: they may be able to estimate what kind of opponent they are facing in a given contest. Indeed, an important reason for the very large number of models of dyadic contests is that animals vary in their cognitive capabilities as well as in the situations they encounter. Depending on the situation, information gathering over behavioural time may be absent or present, and can happen before or during the contest.

Models can therefore be categorised regarding the degree of assessment that influences an animal's decision-making. For example, a war of attrition (section 2.5.2) where an individual's persistence time is picked from an exponential distribution may involve no assessment of how this particular fight might differ from any other. A second set of models is based on self-assessment: for example, an individual may be aware that it is relatively strong, or that it is guarding a resource that it knows to be more valuable than average (this information might not be available for an intruder attempting to acquire this item). Finally, models may also include 'mutual assessment'. Information transfer may occur in the form of damage accumulation during fights (as in the sequential assessment game, section 2.6.3.1), or information may

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be given intentionally before the fight escalates (see section 2.6.4 on signalling). For details of this type of categorisation of models see Arnott and Elwood's (2009) review.

It is not surprising that models in which information transfer occurs over behavioural time tend to be of an 'open box' type. There are exceptions; for instance, a theoretical study of 'badges of status', i.e. the idea that individuals do not engage in a fight before they have assessed each other's RHP based on a relatively cost-free 'badge' trait, might model the entire interaction as a single step (e.g. Johnstone & Norris 1993).

2.5 The beginning: ESS and the conundrum of limited war

The dawn of game-theory models of animal contests occurred simultaneously, indeed in the same publications, with the development of the concept of evolutionary stability. The precursors of the evolutionarily stable strategy arose in the different context of sex ratios (see Fisher 1930 for classical sex ratio theory, and Hamilton 1967 for an 'unbeatable strategy' for sex ratios under local mate competition; for more on history see Maynard Smith 1976, 1982, p. 174). The very next step was to develop these concepts to present a formal definition of the evolutionarily stable strategy, or ESS, in the context of animal contests (Maynard Smith & Price 1973, Maynard Smith 1974). By definition, if a population adopts the ESS, then it cannot be invaded by any other strategy that is initially rare (here the ESS differs slightly from the concept of the Nash equilibrium: it is possible that a strategy is a Nash equilibrium but not an ESS, which happens if competing strategies achieve equally high payoffs). Mutants or immigrants using a different strategy therefore cannot spread in the population (formal definitions are provided by Maynard Smith 1982, Mesterton-Gibbons 2000, McGill & Brown 2007).

What this means in practice was illustrated by Maynard Smith and Price (1973), who developed two models, both inspired by animal contests and their puzzlingly constrained form ('limited war'). This paper inspired two different mathematical routes to analysing conflict: the Hawk–Dove framework and the war of attrition.

2.5.1 Hawks and Doves

In their first model, Maynard Smith and Price (1973) presented what became a precursor of the later Hawk–Dove game. Unlike later, simplified Hawk–Dove models, Maynard Smith and Price's (1973) was an 'open box' model, where individuals played repeated moves until one of them retreated, either by choice or due to serious injury. Because of the great variety of responses one can imagine to a long sequence of events (e.g. 'I will always play Hawk except I will retreat if the fight has taken more than 122 steps and I have accumulated a damage level of at least 0.23'), there is an infinite number of potential strategies of which Maynard Smith and Price (1973) analysed only five. This highlights a feature of ESS models that one should be aware of: stability is analysed by asking whether invaders (mutants or immigrants) using a deviating rule can spread, and one has to choose the set of potential deviations in a biologically meaningful way. To take an extreme example, if a creature was able to evolve a machine gun this would change the rules of the game and easily destroy earlier stability (Davies 1979). The general point is that stability is assessed only with respect to alternatives that are judged to be realistic, not with respect to every conceivable improvement. The set of possible strategies is decided by the modeller and this decision should be subject to biological scrutiny.

In Maynard Smith and Price's (1973) model, individuals played a sequence of moves that could belong to the category of conventional moves (which in this context means not escalating), dangerous escalation, or retreat. Among the five analysed strategies some were quite complex, which meant that the authors had to resort to computer simulations to estimate the direction of evolution. As an example of complexity, their 'Prober-Retaliator' occasionally tries escalating dangerously but de-escalates if the opponent escalates in response and the response, when provoked by a fellow prober, is escalation with a high probability.

Maynard Smith and Price (1973) showed why limited aggression can evolve: if very aggressive types ('Hawks') are common, they will almost always encounter other Hawks and injury is a common result. In many situations, gaining access to a particular food item or a particular mate is less important than avoiding injury. In other words, if the value of the resource is V and an injured individual's payoff is $-C$, then $V < C$ predicts that 'Mouse' (which corresponds to 'Dove' in later models) can fare well against a 'Hawk', and 'Prober-Retaliators' can do extremely well. Of course, one can ask how a 'Mouse' can persist if it never acquires any resources. In other words, how exactly

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Table 2.2 The Hawk–Dove–Bourgeois game with uncorrelated asymmetries. The Hawk–Dove game can be extracted on its own by excluding the Bourgeois row and column. Individual fitness is calculated assuming that individuals find themselves in the 'owner' and 'intruder' roles with equal frequency. Often a separate column is added for the paradoxical anti-Bourgeois but its success can be equally viewed from the current table, by noting that the 'Bourgeois' is a simple conventional solution that can refer to any conceivable and easily perceivable asymmetry.

		Opponent		
		Hawk	**Dove**	**Bourgeois**
Self	Hawk	$\frac{V-C}{2}$	V	$\frac{3V}{2} - \frac{C}{4}$
	Dove	0	$\frac{V}{2}$	$\frac{V}{4}$
	Bourgeois	$\frac{V-C}{4}$	$\frac{3V}{4}$	$\frac{V}{2}$

does reproduction take place in a population where a rare Mouse's payoff is close to zero, yet is much better than the population-wide Hawk rule? This is possible because $V < C$ predicts that Hawks have negative fitness. The proper interpretation of payoffs became a recurrent theme in later game-theory models, but the more urgent task was to simplify the Maynard Smith and Price (1973) model (which had many parameters, including fitness consequences of minor injuries such as 'scratches'). Developing a simpler model was desirable in order to capture the minimal, and thus essential, features that could explain why 'limited war' can exist in animal populations.

The model was soon simplified to the classic Hawk–Dove game (Maynard Smith & Parker 1976, Maynard Smith 1982). This game is a 'black box' type model, with individuals playing either 'Hawk' or 'Dove' (Table 2.2). It is easy to see that in a pure population of Doves an incoming Hawk will do very well. It is assumed that Doves retreat without fighting, so in these encounters Hawks take the resource V and Doves gain 0. (If two Doves meet they share resources peacefully, gaining $V/2$, although this can also be interpreted as them 'flipping a coin' to determine which contestant gets the whole resource.) Because $V > 0$, Hawks are favoured by natural selection, but as they now increase in frequency, a focal Hawk will increasingly often meet another Hawk. Hawk–Hawk encounters are not as profitable for Hawks as Hawk–Dove encounters: not only is winning no longer guaranteed, there is now also a risk of injury. The expected payoff in a fight against another Hawk is $(V - C)/2$, less than half of what it was against Doves, V: the more Hawks in the population, the smaller the success of Hawks. To be precise, if the proportion of Hawks in the population is P, the Hawk's expected payoff will be $P(V - C)/2 + (1 - P)V$. This has to be compared against the Dove's expected payoff which is 0 against Hawks and $V/2$ against other Doves. Thus, Hawks will increase in frequency as long as

$$P(V - C)/2 + (1 - P)V > (1 - P)V/2 \quad (2.1)$$

This is true up to the point where $P = V/C$, which is the ESS: a polymorphism where a proportion P of individuals play Hawk and the rest play Dove (or, as an alternative interpretation, each individual chooses to play Hawk with a probability P when participating in a contest: Maynard Smith & Parker 1976). On average, Hawks and Doves will have equal fitness, otherwise natural selection would increase the frequency of one type. If $V/C > 1$, then no such mixed strategy is possible, instead (2.1) is true for all values of P and every individual will play Hawk. This simplified model shows much more clearly than the original (Maynard Smith & Price 1973) why limited war can be stable, and it also predicts when 'total war' (*sensu* Maynard Smith & Price 1973) should take place: the higher the stakes (high V), the more likely it is that aggression evolves, even if its costs, C, are high.

2.5.2 War of attrition

Imagine a game in which you and one other player each make separate but simultaneous telephone calls costing £10 per minute (billed on a per-second basis). As soon as one player hangs up they stop accumulating further charges and the other receives a prize of £1000. How long would your call last?

This is a 'war of attrition'; an accumulating process of unpleasant damage in a two-player context. Both individuals pay costs and the individual who persists longer wins the resource. The telephone contest thought experiment was not used when the model was first presented, but it is very useful to think how one would behave in it. It might appear logical, for example, that no player should ever play beyond running up a bill of £1000. Now imagine that you have accumulated that much damage: is it not tempting to carry on for just a few seconds longer, for you might win it back? Further, would your behaviour depend on whether you believe your ability to withstand losses is lower or higher than that of your opponent?

Maynard Smith and Price (1973) introduced this type of game as their second example of 'limited war', considering a version in which there were no asymmetries between individuals. The players must individually decide on a value, C^*, which is the threshold cost (or damage) they are prepared to accumulate before they retreat. The winner gains the resource of value V. Strategies are of the form 'carry on if $C < C^*$, otherwise retreat'. A common interpretation of the war of attrition is that C increases linearly with time, t, spent in the fight, i.e. $C(t) = ct$ where c indicates the rate of damage accumulation. The analysis can also be made more general by replacing the consideration of time concepts with direct consideration of damage levels (Maynard Smith 1974, Bishop & Cannings 1978).

The interesting feature of this game is that there can be no *pure ESS* (a pure ESS would mean that a player always chooses the same value of C^* without randomness). In this game individuals do not know each other's values of C^*; if they did, it would be easy to win simply by persisting longer by an infinitesimally small amount of time. However, one way for individuals to 'know' the opponent's C^*, despite no actual information transfer upon encounter, occurs if populations converge on a single C^*. Natural selection will then favour individuals who behave as if they knew that all opponents will use C^*, and persist for slightly longer. One might then predict runaway evolution towards ever-increasing C^*, but this cannot carry on forever because if C^* exceeds $V/2$ then a mutant who does not fight at all ($C^* = 0$) will have higher expected fitness (zero) than a player who pays a larger cost than the average gain (cost: C^* each, gain: $V/2$). The statement *there is no pure ESS* means that no value of C^* exists that could prevent some deviating individuals from doing better than the rest of the population. Predictable opponents can be exploited.

Instead, Maynard Smith (1974) showed that there is a *mixed ESS* solution, in which individuals evolve to be maximally unpredictable. In a *mixed strategy*, there is some degree of randomness in individual's actions. For example, a coin-tossing individual 'persists until $C = 1$ with probability 0.5, otherwise persists until $C = 1.2$' gives an opponent a bigger challenge than does a pure strategist. If, however, all individuals in a population use such a strategy, a mutant could exploit the knowledge that its opponent will use very specific persistence times; assuming that V makes it worthwhile, one could play according to the rule 'first persist until $C = 1.001$, then if opponent hasn't given up persist until $C = 1.2001$'. Overall such a strategy is simply captured by $C^* = 1.2001$ and it can easily beat the coin-tossers (assuming $V > 1.1$ because fights will cost $(1 + 1.2)/2$ on average); but if $C^* = 1.2001$ spreads, it could again be beaten using the arguments above.

There is only one strategy that cannot be exploited by mutants who evolve to persist just slightly beyond those values of C that the opponent uses with a high probability. This strategy has a *fixed rate of retreating* if costs accumulate linearly over time (for the more general case of a fixed rate with respect to damage accumulation see Maynard Smith 1974). If all population members use such a rate, then the duration of the contest so far cannot be used to predict how long an opponent is still prepared to carry on, and thus it cannot be exploited. The ESS rate equals c/V in the case of linearly accumulating costs: higher costs predict shorter fights (higher rate of retreating per unit time), higher resource value predicts longer fights (lower rate of retreating per unit time).

Note that the formulation of a 'rate' applies whether $c > V$ or the reverse: it is a continuous-time parameter that can exceed 1 without causing mathematical problems (while retreat *probabilities* of course cannot exceed 1). To see how this works, use the above telephone contest game with $c = 200$ and $V = 100$, i.e. an outrageous charge of £200 per minute and a prize of £100. Intuition tells us that since V is relatively low compared to c, sensible individuals will only make short calls, and this is indeed the case. If populations evolved to play this game we would expect individual call durations to stop at a rate $200/100 = 2$ per unit time (minute). This means that an individual should, on average, be prepared to hold the telephone for 30 s (1/2 min). This rule will not evolve as a fixed, exploitable threshold: the ESS is to pick a duration from an exponential distribution that has the mean 0.5 min. The exponential distribution is the mathematical solution for the expected 'lifespan' of an entity (a telephone call, or a contest) that 'dies' at a constant rate.

Thus, the ESS in the symmetric war of attrition with linearly increasing costs can be formulated as 'at any point during the fight retreat at a rate c/V' or, equivalently, 'pick the persistence time t^* from an exponential distribution that has the mean V/c, i.e. $P(t^*) = c/V \exp(-ct^*/V)$'. The cost an individual is prepared to accept before retreating is ct^* and this too is distributed exponentially, with a mean V. This latter result can be shown to hold generally, without having to make an assumption of linear damage accumulation over time (Maynard Smith 1974; for an