OWNERSHIP CONFLICTS AND THEIR RESOLUTION

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CANDIDATES DECLARATION

I declare that the work recorded in this thesis is entirely my own, except where otherwise stated, and that it is of my own composition. Much of the material included in this thesis has been produced in co-authorship with others and has been presented for publication. My personal contribution to each chapter is as follows:

2. *Published as*: Morrell, LJ, Backwell, PRY & Metcalfe, NB **Fighting in fiddler crabs *Uca mjoebergi*: what determines duration?** *Anim. Behav.* (in press). The idea was developed by PB and LM. LM carried out all data collection and the majority of the statistical analysis and was senior author on the manuscript.
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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUMMARY

Game theory has been used to investigate a wide range of evolutionary questions, and has been important in explaining apparently selfish patterns in animal behaviour, and behaviours that do not appear to benefit the individual. The modelling chapters in this thesis develop new game theory approaches to modelling animal conflict, investigating the acquisition of territories and the trade-offs that occur between behaviours.

Many game theory models of conflicts between individuals make predictions regarding the duration of fights in relation to asymmetries in resource holding potential (RHP). Duration is often interpreted as a result of mutual assessment of RHP, allowing the weaker individual to avoid costly interactions. However, the duration of a contest may also be the result of each individual persisting to a threshold determined by its own RHP. In fiddler crabs, *Uca mjoebergi*, I show that duration of contests increases with increasing size of the loser, and decreases, but to a lesser extent, with increasing size of the winner, suggesting that neither the mutual assessment or individual threshold hypothesis can explain fight duration in this species. Instead, individual cost thresholds may determine duration, but larger opponents may inflict costs more rapidly, consistent with the cumulative assessment game of animal conflict.

In animal contests, the larger opponent is often victorious, but contests are often initiated by individuals that have little chance of winning (generally smaller individuals). A number of hypotheses may explain this behaviour, including a lack of alternative options (the 'desperado effect'). Recent work has suggested that likely losers attack first due to an error in perception: they mistakenly perceive their chances of winning as being greater than they are. Using a game theoretical model, I show that if smaller individuals can accurately assess their chance of winning, if this chance is relatively high, and if they have few alternative options, they are predicted to be as aggressive as their larger opponents. In addition, when resources are abundant, and small individuals have some chance of winning, they may be more aggressive than their larger opponents.

Many game theory models of animal contests consider the evolution of fighting when the winner claims the resource. An alternative hypothesis suggests that space can be divided if animals avoid areas where they have been involved in aggressive interactions. Using a game theory model, I show that avoidance of a single fight location can be adaptive if the benefits of access to the area are low compared to the costs of fighting. If this is not the case, then one individual (typically the winner) returns to the area to claim the resource, while the other (the loser) avoids it. In a spatially realistic model, where space must be divided between competitors, avoidance behaviour is adaptive when the costs of fighting are high and the population density is low, and well-defined, exclusive territories are formed. Low fight costs and high population densities lead to the break down of territoriality and the formation of large, overlapping home ranges.

Paradoxical solutions to contests over the acquisition of indivisible space, where owners retreat when challenged by intruders, are found when asymmetries in RHP are small or absent. In the game theory approach to spatial division, paradoxical strategies are stable when asymmetries between the contestants are small, when individuals adhere strictly to behavioural rules, and when the ancestral population used a paradoxical strategy. In the spatially realistic approach, a novel reason why paradoxical strategies do not exist in nature emerges. Fights may end without a clear winner or loser, and draws may be common. When this is the case, a common-sense strategy is often more adaptive than the paradoxical alternative.

Individuals may face conflicts of time or energy, when they are faced with a choice of which of two or more mutually incompatible behaviours they can perform. Time allocated to two such behaviours may trade-off in a counterintuitive way. Intuition suggests that the time invested in performing a behaviour should decline as the individual's ability to perform the behaviour increases, but this may not always be the case. Instead, investment in one behaviour is shown to first increase and then decrease as ability increases. This could have implications for the empirical study of trade-offs as it may appear that individual ability has no effect on the trade-off under consideration.

Animals often compete for limited resources, and this competition can have fundamental implications for population dynamics. Mate choice favours males who outperform others in securing resources, but the effects of resource depletion have rarely been discussed in the context of sexual selection. If males compete for resources used in sexual displays, I show that intense female preference for high quality displays can reduce display quality. This is because males benefit from excluding others from resources, damaging the overall efficiency of resource use in the population, and leading to poorer prospects for efficient female choice.

In socially monogamous birds, males are able to protect their paternity by guarding their social mate, and preventing her from seeking extra-pair copulations. Thus, the paternity gained by a male depends both on the intensity with which females seek extra-pair copulations, and the guarding behaviour of males. The relationship between evolutionary stable guarding behaviour and the risk of cuckoldry can be complex and non-linear. Attractive males are generally predicted to guard less than unattractive ones, but within-pair paternity may correlate either positively or negatively with the number of extra-pair offspring fertilised by a male. Negative correlations, where attractive males are cuckolded more than unattractive ones, become likely if female extra pair behaviour is due to factor applicable to most females (e.g. fertility assurance) rather than the subset mated to unattractive males (e.g. good genes).

There have been a number of recent developments in game theoretical techniques, which have the potential for increasing our understanding of animal behaviour and providing better matches for observed data where this is required. These techniques provide useful avenues of further research in game theoretical modelling of different systems, including those in this thesis.

CHAPTER 1

GENERAL INTRODUCTION

In this thesis, I consider the general theme of ownership conflicts. In **chapters 2** to **5** of this thesis, I consider conflicts between individuals, in the form of contests over territories and other limited resources. In **chapters 6** to **8**, I will discuss conflicts that occur within an individual who is the owner of a resource, when the individual must allocate time or energy between two or more mutually incompatible behaviours.

Animal behaviour can be thought of as the outcome of a series of trade-offs between the costs and benefits associated with performing various actions. A central tenet of behavioural ecology is that animals are expected to maximise net benefits, measured in units of fitness; a process that leads to optimal behaviour. Therefore studying these trade-offs can improve our understanding of the way animals behave. For example, early optimisation studies of the size of animal territories phrased the question of how large territories should be in terms of the costs of defending those territories against intruders, traded off against the benefits to be gained from monopolisation of the resources they contained (e.g. Hixon 1980; Schoener 1983; reviewed in Adams 2001). However, most of these models assumed that animals were free to adjust their territory boundaries without constraint from neighbours (Grant 1997; Adams 1998; Keeley 2000). In reality, contiguous territories may be compressed below their optimal size by the pressure exerted by neighbours, and thus the behaviour of other individuals is also important when considering territoriality. When considering how individuals in a population should respond to the behaviour of the other population members, game theory modelling is needed.

The theory of games was first developed by von Neumann and Morgenstern (1953) in reference to human economic behaviour. The concepts were first explicitly applied to evolutionary biology by Lewontin (1961), who pictured a species playing a game against nature, and aimed to find the strategies that minimised the risk of extinction (Maynard Smith 1982). Game theory can provide an important tool in understanding any situation in which an individual's success depends not only on that individual's own behavioural choices but also on the decisions of others. The central concept of evolutionary game theory, the evolutionarily stable strategy (ESS), was introduced by Maynard Smith and Price in 1973. An ESS is a strategy (behavioural phenotype), which, if adopted by all members of a population, cannot be invaded by a mutant strategy (an alternative behavioural phenotype) under the influence of natural selection (Maynard Smith 1982).

The first application of evolutionary game theory to a biological phenomenon dealt with the problem of animal conflict. Among the questions answered by game theory include the problem of why animal conflicts are often settled by conventional behaviour, rather than by injurious fighting. Maynard Smith and Price (1973) demonstrated that conventional behaviour can be explained in terms of the selfish interests of the individual contestants, clearly demonstrating that animal conflict can be explained in terms of individual costs and benefits rather than 'good-of-the-species', group selectionist, arguments.

Both optimisation and game theory approaches to modelling territorial behaviour (see above) have produced testable predictions, and in many cases their findings have been supported by empirical investigation. In order to find the optimal behaviour of individuals in the different situations I consider, I use a combination of optimisation (**chapter 6**) and game theory (**chapters 3, 4, 5, 7** and **8**) approaches. I will now discuss the background to each chapter in this thesis, including the existing theory and empirical approaches that lead to each of the questions investigated.

Conflicts over ownership

In the first chapters of this thesis, I consider conflicts between individuals competing for resources, generally territories. I look at fights between individuals for ownership of an existing territory, and investigate the question of how space is divided to form territories.

ACQUIRING TERRITORIES

Competition to obtain a territory is a major determinant of fitness in territorial animals. Ownership of a territory may be a prerequisite to breeding, or essential for foraging. The individuals that win in fights for territory ownership tend to be those that already own the resource, are larger, or have more to gain or lose (e.g. Davies 1978; Krebs 1982; Turner & Huntingford 1986; Enquist et al. 1990; Marden & Waage 1990; Beaugrand et al. 1996; Edsman & Jonsson 1996; Jennions & Backwell 1996; Petersen & Hardy 1996; Tobias 1997; Brandt 1999; Johnsson et al. 1999; Johnsson et al. 2000; Wenseleers et al. 2002). These factors combine to produce an individual's resource holding potential, or RHP (Parker 1974a), a measure of an individual's capacity to win a fight against an opponent. Much of the theory applied to the study of how animals obtain exclusive use of space stems from game theoretical models developed to study animal conflicts. The models are used to investigate the outcome of contests for indivisible resources, in which the winner of the contest gains sole use of the resource. Four important models applied to the study of territory acquisition are the hawk-dove game (Maynard Smith & Price 1973, Maynard Smith 1979; Maynard Smith 1982), the war of attrition (Maynard Smith 1974; Bishop & Cannings 1978, Hammerstein & Parker 1982), the sequential assessment game (Enquist & Leimar 1983, 1987; Leimar & Enquist 1984) and the cumulative assessment model (Payne 1998). These models describe pair-wise contests between two opponents, and investigate ESSs for territory acquisition.

1. Hawk-Dove Game

In the classic hawk-dove game (Maynard Smith & Price 1973; Maynard Smith 1979; Maynard Smith 1982) the behavioural options available to an individual are 'hawk' (escalate until injured or opponent retreats) and 'dove' (display, but retreat if opponent escalates). In the early models, competitors were identical (e.g. they were of the same body size), and it was assumed that there was a finite set of discrete strategies, a model too simple to have any real-world validity. Complexities have since been added including conditional strategies based on role asymmetries (owner or intruder) such as 'bourgeois', where owners attack (play hawk) and intruders retreat (play dove; Maynard Smith & Parker 1976; Maynard Smith 1979). It is from this that the idea of the 'paradoxical ESS' has emerged: in this case, owners retreat in the face of attacking intruders, thus giving up their territories without a fight. Other complexities that have been added include asymmetries in the value of the resource to the two competitors, assessment of asymmetries in resource holding potential, and extended contests involved repeated interactions (Hammerstein 1981; Mesterton-Gibbons 1992; Mesterton-Gibbons & Adams 1998; Crowley 2000). These additions increase the general validity of the game, particularly with respect to paradoxical strategies.

2. War of Attrition

The war of attrition (WOA) is another classical game, which asks how long a contestant should display or fight over a disputed resource, given that the winner is the one that persists for longest (Maynard Smith 1974; Bishop & Cannings 1978; Riechert 1998). In the asymmetric war of attrition, individuals adopt different roles (such as owner and intruder), and the cost of displaying (*k*, set by the individual's RHP) and value of the resource (*V*) may differ between them. The individuals assess their ratio of *V*/*k* relative to that of their opponent, and the game allows for error in this assessment (Hammerstein & Parker 1982; Bradbury & Vehrencamp 1998). Escalated contests occur when both individuals perceive themselves as likely winners of the contest. More recent developments of the WOA include the energetic WOA (Payne and Pagel 1996, 1997; Payne 1998) and the WOA without assessment (Mesterton-Gibbons et al. 1996). These models base persistence bids on the RHP of the individual, and assume that no assessment of the size of the opponent needs to take place.

3. Sequential Assessment Game

In the sequential assessment game (SAG, Enquist & Leimar 1983, 1987; Leimar & Enquist 1984; Enquist et al. 1990), fights consist of a sequence of behaviours; at each step in the sequence the contestants assess their relative strength and each of them decides whether to give up or to continue to fight based on these assessments. The SAG assumes that opponents gain additional information about RHP asymmetries with each consecutive exchange of actions, and the error in assessment decreases as the contest continues. The greater the asymmetry, the more quickly the error in assessment will decrease and result in a contest of short duration. Extended contests are predicted when the asymmetry between the contestants is low. Fights are expected to follow a predictable sequence of escalation, with each fight element being more intense than the preceding one (Enquist & Leimar 1983, 1987; Leimar & Enquist 1984; Enquist et al. 1990).

4. Cumulative Assessment Model

In the cumulative assessment model (CAM), developed by Payne (1998), each individual has a threshold of costs that it is willing to accrue in a contest (determined by their RHP), and costs accrue as the result of actions by the rival. An individual's decision to persist or retreat is based on a cumulative sum of its adversary's actions, and superior rivals may inflict higher costs than rivals of lower quality. Contests are resolved quickly when individuals with low thresholds compete against rivals who are able to inflict higher costs, but contests escalate when the eventual loser has high cost thresholds.

Empirical studies of the duration of contests have shown a great deal of support for the SAG as a model of animal conflict, finding that contest duration increases as the asymmetry in RHP between the individuals decreases, or that relative size is the best predictor of contest outcome (Englund & Olsson 1990; Enquist et al. 1990; Faber & Baylis 1993; Marden & Rollins 1994; Smith et al. 1994; Dale & Slagsvold 1995; Jennions & Backwell 1996; Hack et al. 1997; Moya-Laraño & Wise 2000; Renison et al. 2002; Pratt et al. 2003). Some studies exist, however, which suggest some support for models based on individual thresholds (namely the energetic WOA, Payne & Pagel 1996, 1997; Payne 1998) and the WOA without assessment, Mesterton-Gibbons et al. 1996), where contest duration increases with size in contests between size-matched competitors (Dixon & Cade 1986, Glass & Huntingford 1988, Foster 1996; Jennions & Backwell 1996, Whitehouse 1997). However, recent modelling work suggests that the pattern of decreasing duration with increasing difference in size between competitors, commonly cited as support for the SAG, would also be seen if duration depended on the RHP of the eventual loser (Taylor & Elwood 2003). Taylor and Elwood (2003) suggest that many of the studies seeming to support the SAG may be incorrectly interpreted, as the authors of those studies failed to consider the RHP of the loser as an independent predictor of contest duration. In **chapter 2**, I report the results of an empirical study investigating the factors determining the duration of contests over burrow ownership in the males of the Australian fiddler crab *Uca mjoebergi* (Figure 1.1). The chapter attempts to distinguish whether persistence is based on individual thresholds or mutual assessment of relative RHP, and thus considers which of the models are most appropriate when describing contests within this species.

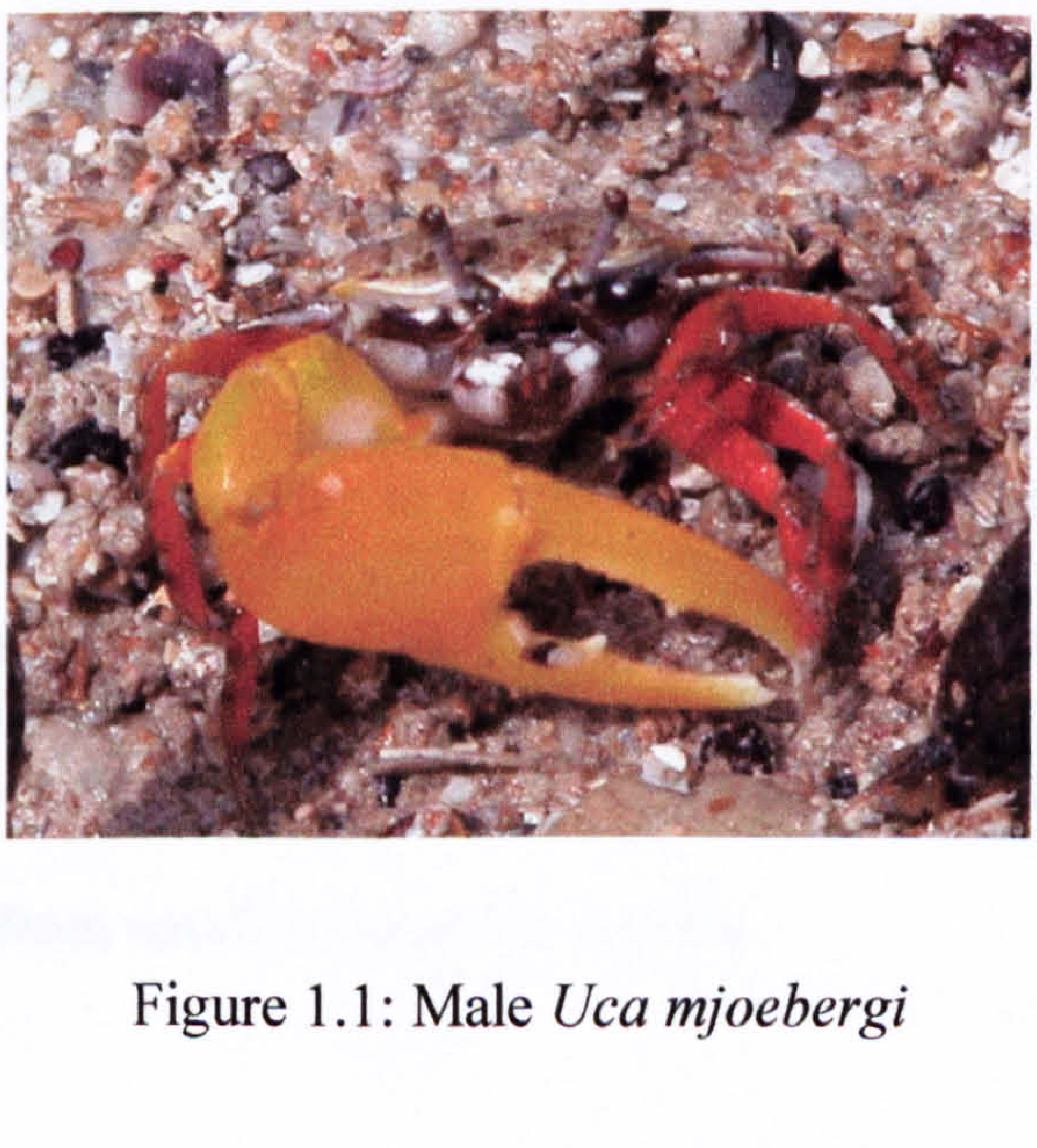


Figure 1.1: Male *Uca mjoebergi*

Game theory models of animal contests predict that individuals of low RHP are able to assess their relative inferiority in a contest and retreat accordingly, and thus aggression is expected in larger individuals but not in smaller ones. Although there are many examples of larger individuals acting aggressively towards smaller ones (e.g. Zack 1975; Brace & Pavey 1978; Dowds & Elwood 1983; Figler & Einhorn 1983; Barlow et al. 1986; Turner & Huntingford 1986; Lindström 1992; Keeley & Grant 1993; Thorpe et al. 1994), there are also cases where aggression is predominantly initiated by the smaller competitors (Dow et al. 1976; Enquist & Jakobsson 1986; Ribowski & Franck 1993; Smith et al. 1994; Morris et al. 1995; Moretz 2003).

Smaller individuals may act aggressively for a number of reasons, including asymmetries in the value of the resource to the two competitors (Davies & Houston 1981; Shutler & Weatherhead 1992; Eason & Hannon 1994; Johnsson et al. 2000; Johnsson & Forser 2002), an increased probability of winning for the individual that attacks first (Jackson 1991; Figler et al. 1995; Hack 1997; Martin et al. 1997; Taylor et al. 2001; Roeder et al. 2002), a lack of alternative options (the desperado effect; Grafen 1987) and misperception of either themselves as being larger than their opponent (Bradbury & Vehrencamp 1998) or their chances of winning as being higher than they actually are (Just & Morris 2003). In **chapter 3**, I develop a model investigating whether it is necessary to invoke perception errors or asymmetries in costs and rewards to explain aggression. In the chapter, competitors can accurately perceive their chances of winning in a fight, and I explore the conditions under which aggression is directed from small to large individuals.

While the standard game theory models discussed previously are appropriate to contests over established territories and indivisible resources, the process of territory formation may more resemble bargaining and negotiation, rather than winner-takes-all fights (Maynard Smith 1982; Stamps & Krishnan 1995, 1998, 1999, 2001). An alternative approach to modelling the acquisition of territories has recently emerged, using local rules of movement and interaction to predict space use by adjacent residents (Adams 2001). Examples of such mechanistic models of territory acquisition include models of movement and scent marking to predict spatial patterns in timber wolves (*Canis lupus*, Lewis & Murray 1993; White et al. 1996), and the formation of juvenile *Anolis aeneus* lizard territories as a learning process governed by an individual's experiences in different locations (Stamps & Krishnan 1999; 2001). Stamps and Krishnan's (1999; 2001) models of territory formation suggest that space can be gained through 'nagging' rather than decisive fights, and that animals newly arriving in a territory can divide space between them through two processes: familiarity with an area increases the individuals' use of a particular location, but aggressive interactions decrease use of that location (Stamps & Krishnan 1999, 2001; Sih & Mateo 2001). These models (and other mechanistic models) differ from game theory models in one fundamental way: they do not assess the adaptiveness of the behaviours on which they are based, that is, they do not analyse the costs and benefits of the behaviour. In **chapter 4** I use a game theory approach to investigate whether the avoidance behaviour on which Stamps and Krishnan's (1999, 2001) models are based is adaptive, investigating the ESS probabilities for an individual to return to a single contested area following a fight, under various conditions of costs, benefits and adherence to behavioural rules.

Currently, no model of fights between individuals exists that combines realistic two-dimensional division of space (a typical feature of mechanistic models) with arguments of evolutionary optimality (found in game theory models). Approaches to the division of space have considered only the winning of a single patch of habitat as a potential extension to a individual's territory (**chapter 4**), or the question of how individuals can negotiate the division of a line (one dimensional habitat) into two territories (Maynard Smith 1982; Lewis & Moorcroft 2001; Mesterton-Gibbons & Adams 2003; Pereira et al. 2003), and do not explicitly model two-dimensional space. In **chapter 5**, I develop a model that addresses the issues of multiple competitors and continuous, two-dimensional space, while investigating the adaptiveness of four different strategies for territory acquisition. This chapter combines the spatially explicit approach of mechanistic models with some of the evolutionary aspects of game theory models, continuing to investigate the stability of the avoidance strategies for territory acquisition proposed by Stamps and Krishnan (1999; 2001), and discussed in **chapter 4**.

PARADOXICAL STRATEGIES

A further question addressed in **chapters 4** and **5** is that of paradoxical strategies. These strategies emerged from early hawk-dove games of territorial contests, and suggest (in contrast to the 'common-sense' solution) that intruders, individuals of lower RHP or individuals with less to gain are more likely to win contests than their better equipped opponent. Paradoxical strategies are extremely rare in nature (see Burgess 1976; Fernet & Smith 1976; Peeke et al. 1998 for possible examples), and thus it is important to develop modelling approaches that explain why this is the case, i.e. to develop models that do not predict that the paradoxical alternative to a common-sense solution can be an ESS. Maynard Smith and Parker (1976) recognised the problem of the paradoxical ESS, and developed extensions of the hawk-dove and war of attrition games. They concluded that paradoxical solutions are only favoured under limited conditions, and are likely to be rare in nature because there is always an alternative, common-sense ESS that can evolve from a greater range of starting conditions. Further work continues to predict paradoxical solutions if RHP or resource value asymmetries exist but are small enough (Hammerstein and Parker 1982; Maynard Smith 1982; Enquist and Leimar 1987; Mesterton-Gibbons 1992; Mesterton-Gibbons and Adams 1998; Field and Hardy 2000; **chapter 4**), except when making *a priori* assumptions that render the common-sense strategy stronger and more likely to prevail (Mesterton-Gibbons 1992). The attempt to 'explain away' paradoxical strategies seems to have been successful: the current interpretation by empiricists is that paradoxical strategies are theoretically close to impossible (Field & Hardy 2000; but see Kemp & Wiklund 2001).

In addition to asking how animals can divide space, **Chapters 4** and **5** investigate the conditions under which a paradoxical strategy for dividing space (a different situation to that in the hawk-dove game, in which paradoxcial strategies have been extensively studied) can be adaptive. In **chapter 4**, a paradoxical strategy is one in which an individual is more likely to return to a contested area after losing a fight than after winning one, and I investigate the effects of RHP asymmetry and behavioural variability on the stability of such a strategy, and show that paradoxical solutions can exist when RHP asymmetries are small enough, and animals adhere strictly to behavioural rules.

However, in the absence of RHP asymmetries, the common-sense and paradoxical strategies become equivalent (unless there is some other asymmetry such as residency which could determine fight outcome). Where RHP asymmetries do not exist, 'winning' and 'losing' are labels that denote the outcome of a fight, but give no information on the fighting ability of the individuals (when asymmetries do exist, the winner of a fight is likely to be of greater fighting ability than the loser). In this situation, the paradoxical strategy (where losers gain resources at the expense of winners) should find itself a niche. In **chapter 5**, I investigate whether a paradoxical strategy can be stable in the absence of RHP differences (which are not included in the model), and offer a solution unrelated to such differences. Winning and losing are not the only possible outcomes of a fight: fights may also end up in a draw, without a clear winner and loser (Stamps & Krishnan 1994a,b, 1997, 1998, Adams 1998, Stamps 1999). In this case, a paradoxical strategy must mirror the common-sense one in its response to draws, as well as wins and losses, and I investigate whether this creates an asymmetry which renders the common-sense strategy more likely to persist that the paradoxical one, even in the absence of RHP or resource value asymmetries.

Conflicts faced by the owner of a resource

The second part of the thesis considers the general theme of conflicts faced by an individual, who is the owner of a resource, when chosing between two or more mutually exclusive behaviours.

Many behaviours are seen as a trade-off between the costs and benefits of the action: when defending a territory, an owner may base its response to an intruder on the quality of the resource at stake and/or their own fighting abilities (e.g. Jennions & Backwell 1996; Beaugrand et al. 1996; Petersen & Hardy 1996; Johnsson et al. 1999; Alcock & Bailey 1997), thus trading-off the costs of fighting against the benefits gained from retaining the territory. Game-theoretical models of aggressive base an individual's decisions to attack or retreat on the respective benefits and costs of the different approaches when asymmetries between the opponents exist (Maynard Smith & Parker 1976, Hammerstein & Parker 1982, Enquist & Leimar 1987, Mesterton-Gibbons 1992). Parental care is often thought of as a trade-off between current and future reproduction (Webb et al. 2002), but in choosing the amount of time or effort to invest in caring for offspring, parents are limiting the amount of time they can spend foraging (Komdeur & Kats 1999) or seeking to produce further offspring through additional copulations (Magrath & Elgar 1997, Szekely & Cuthill 2000), and thus face a trade-off between two or more behaviours within a given breeding attempt. The trade-off between feeding and watching for predators (vigilance) has been intensively studied, and theory predicts that the optimal solution simultaneously balances predator detection and intake rates (Krause & Ruxton 2002). When individuals are faced with a choice between mutually incompatible behaviours that could potentially be performed at any given time, the solution to the trade-off between those behaviours can have fundamental consequences for their fitness.

Territorial defence and mate searching behaviours trade off with predator avoidance, and have been found to alter as the risk of predation increases (e.g. Jennions & Petrie 1997; Candolin & Voigt 1998; Koga et al. 1998). For example, courtship displays involving conspicuous behaviours are reduced when courting individuals perceive a greater risk of predation (e.g. Endler 1987; Sih et al. 1990; Godin 1995; Fuller & Berglund 1996). Thus, the behavioural decisions made by the owner of a resource can have fundamental impacts on their fitness, and one should expect the conflicts between these behaviours to be resolved optimally. In **chapter 6**, I present a general optimisation model that investigates the trade-off decision faced by an individual when allocating time or energy to two behaviours. Specifically, I ask how much of their available time individuals should invest in each activity when their ability to perform the necessary behaviours varies. I illustrate the model with several examples, including a trade-off between courtship and defence behaviours (Candolin 1997; Santangelo et al. 2002), and between these behaviours and predator detection and avoidance behaviour (Sih et al. 1990; Fuller & Berglund 1996; Godin 1995).

The acquisiton of resources is essential to survival. In the early chapters of this thesis, I consider contests for territory ownership, but where each resource item is of lower value (e.g. a single food item), resources can be acquired in a different way. Foraging indivduals can search for food items themselves, or steal resources from others (kleptoparasitism). This has been studied extensively in 'producer-scrounger' games of foraging individuals (e.g. Barnard & Sibly 1981, Vickery et al. 1991, Giraldeau & Beauchamp 1999, Giraldeau & Caraco 2000). In these games, individuals can either search for food (producers) or search for other individuals that have located food (scroungers), but cannot do both simultaneously (Barnard & Sibly 1981; Vickery et al. 1991). The frequency of scroungers in the population decreases the rate at which food can be discovered, and hence decreases the benefits that can be gained (Parker 1984).

Obtaining mates is a fundamental part of the life of any sexually reproducing organism. In many species, males compete to obtain access to females, and females base their choice of male on some aspect of the male which is believed to indicate his quality and/or the benefits he can provide. Such benefits range from his ability to provide care for offspring (direct benefits of sexual selection; Møller & Jennions 2001) to the quality of his genes which could be passed on the the offspring (indirect benefits; Fisher 1930; Zahavi 1975; Jennions et al. 2001; Kokko et al. 2003). Competiton between males to attract mates has been well studied, is well known to have strong effects on their displays (Andersson 1994). However, the idea that males could interfere directly with each other's displays has received less attention. In **chapter 7**, I consider the effects of theft in a sexual context. The model is phrased in terms of male bowerbirds searching for items with which to decorate their bowers and thus attract females (e.g. Borgia 1985; Borgia & Mueller 1992; Borgia 1995; Madden 2003). **Chapter 7** also considers the question of time allocation by the owner of a particular resource, the bower. In this chapter I consider the proportion of time a male should allocate to searching, raiding and bower defence behaviours, as these behaviours are likely to be mutually incompatible and therefore trade-off against one another.

Reproduction involves conflicts of interest between the sexes. Males can increase their reproductive success by mating with a large number of females, and females by mating with carefully selected, high quality males (reviewed in Chapman et al. 2003; Pizzari & Snook 2003). In socially monogamous birds, females have been shown to actively seek extra-pair fertilisations (Westneat et al. 1990; Petrie et al. 1998; Griffith et al. 2002), a strategy with a number of potential benefits (Jennions & Petrie 2000). If females are mating outside the pair bond, a male should endeavour to protect his paternity and avoid being cuckolded, that is, avoid providing care to the offspring of another male. One mechanism by which males may be able to prevent cuckoldry is to guard their mate and prevent her from engaging in copulations with other males. Mate guarding has been extensively studied in crustaceans and insects (e.g. Grafen & Ridley 1983; Carroll 1993; Plaistow et al. 2003; Härdling et al. 2004), but is less well studied in vertebrates. Although empirical descriptions are common (e.g. Birkhead & Biggins 1987; Møller 1987; Burke et al. 1989; Morton et al. 1990; Johnsen et al. 1998; Chuang-Dobbs et al. 2001), the theoretical background is sparse. In invertebrates, pre- or post-copulatory mate guarding is achieved by maintaining continuous physical contact, but this is impossible for vertebrates, and here males maintain proximity to their females, and thus are able to fend off intruders or prevent the female from seeking potential extra-pair mates.

The benefits associated with avoiding cuckoldry select for guarding behaviour (Van Rhijn 1991; Fishman et al. 2003). However, if females are mating outside the pair bond, this implies that males have fitness opportunities away from their own social mate, which could potentially select for males who maintain less physical proximity to their mate. Males can thus maximise their within-pair paternity by guarding their social mate, but can maximise their extra-pair paternity by not guarding and seeking extra-pair copulations instead. As such, males face a trade-off, as they cannot simultaneously maximise both within- and extra-pair paternity (Hasselquist & Bensch 1991). In **chapter 8,** I investigate how this conflict might be resolved, and develop general predictions on mate guarding and patterns of parentage in socially monogamous species.

In **chapter 9,** I summarise the main findings of **chapters 2** to **8,** and discuss how they relate to general principles of game theory. I make a number of suggestions as to how the work in this thesis could be extended, discussing recent developments in game theory modelling that have provided new and interesting avenues of research, and how these could be used in to further explore and develop the preceding chapters.

CHAPTER 2

FIGHTING IN FIDDLER CRABS *UCA MJOEBERGI*: WHAT DETERMINES DURATION?

Abstract

The duration of a contest between two individuals is often interpreted as being a consequence of mutual assessment of the difference in their resource holding potential (RHP), allowing the inferior individual to avoid costly interactions it is likely to lose. Contest duration is thus predicted by the relative size of the competitors, and increases as the difference between them decreases. An alternative hypothesis suggests that each individual persists in accordance with thresholds determined by its own RHP, and weaker rivals retreat due to their having lower thresholds. Contest duration depends on the RHP of the contestant that gives up first (the loser). Recent work suggests that even though duration is determined by the size of the loser, this hypothesis also predicts a negative correlation between duration and the relative RHP of the contestants. However, it predicts (unlike the mutual assessment hypothesis) that contest duration should increase with the mean size of the contestants. Here, we present the results of a study investigating the determinants of fighting duration in the fiddler crab *Uca mjoebergi*. In this species, fight duration increases with increasing size of the loser, and decreases, but to a lesser extent, with increasing size of the winner. Fights between closely size-matched individuals increase in duration with increasing mean size of the competitors. Neither the mutual assessment or own-RHP dependent persistence hypotheses can accurately explain the data. Instead, we present a modification of recent modelling work, and suggest that in *U. mjoebergi* individual cost thresholds may determine duration, but that larger opponents may inflict those costs more rapidly, consistent with the cumulative assessment game of animal conflict.

Introduction

Differences in resource holding potential (RHP; Parker 1974a) play an important role in determining the outcome of contests for territory ownership. Body size is often used as an indicator of RHP (e.g. Beaugrand et al. 1996; Jennions & Backwell 1996; Petersen & Hardy 1996; Johnsson et al. 1999), but other factors may contribute to RHP, including asymmetries in residency (Davies 1978; Jennions & Backwell 1996; Chellappa et al. 1999; Johnsson et al. 1999; Wenseleers et al. 2002), resource value (Krebs 1982; Alcock & Bailey 1997; Tobias 1997; Johnsson & Forser 2002), energy reserves (Marden & Waage 1990; Marden & Rollins 1994), body condition (Fitzstephens & Getty 2000), age (Kemp 2003), and prior experience of winning or losing (Beaugrand et al. 1996; Hsu & Wolf 2001).

These factors may also be important in determining the duration of fights between individuals. Individuals may avoid extended and costly contests by assessing their own RHP relative to that of their rival, before making a decision as to how to proceed (the 'mutual assessment hypothesis'). The ability for rivals to assess their relative sizes has been incorporated into models of animal conflicts, including some war of attrition games (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982) and the sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990). Asymmetries between individuals can lead to quick resolution of contests based on those asymmetries, but when competitors are evenly matched, escalated fighting results (Maynard Smith 1982; Enquist & Leimar 1983). Many empirical studies have tested, and found support for these models, finding that contest duration increases as some measure of the difference between competitors in RHP decreases (e.g. Englund & Olsson 1990; Enquist et al. 1990; Leimar et al. 1991; Faber & Baylis 1993; Marden & Rollins 1994; Smith et al. 1994; Dale & Slagsvold 1995; Jennions & Backwell 1996; Hack et al. 1997; Moya-Loraño & Wise 2000; Renison et al. 2002; Pratt et al. 2003).

More recent game-theory approaches to modelling contest dynamics have included the possibility that contest duration and escalation could be determined by the size of one (usually the size-disadvantaged) of the competitors (war of attrition without assessment: Mesterton-Gibbons et al. 1996, energetic war of attrition: Payne & Pagel 1996, 1997; Payne 1998). If each individual involved in an energetically costly contest has a threshold level of costs they are willing to accumulate, determined by that individual's RHP, a contest will persist until the individual with the lowest costs threshold reaches that level, and thus duration will be determined by the RHP of the eventual loser. Under the 'own-RHP dependent persistence hypothesis', no assessment of the size of the opponent need take place. Support for these models includes situations where the escalation probability or duration of a contest between size-matched rivals is positively associated with body size (Dixon & Cade 1986; Glass & Huntingford 1988; Foster 1996; Jennions & Backwell 1996; Whitehouse 1997). Fight duration in orb-web spider (*Metellina mengei*; Bridge et al. 2000) and jumping spider (*Plexippus paykulli*; Taylor et al. 2001) contests, and escalation in fallow deer (*Dama dama*; Jennings et al. 2004) are better predicted by the size of the loser than measures of relative size, supporting the own-RHP dependent persistence hypothesis.

Taylor & Elwood (2003) have recently shown using simulation models that a strong correlation exists between measures of relative size and duration of fights even when individual thresholds actually determine contest duration. In addition, there is a strong correlation between smaller rival size and duration when mutual assessment determines duration. Thus, careful examination of data is needed to discover the true determinant of fighting duration (loser RHP or mutual assessment). The models suggest that by considering the direction of the correlation coefficients between the sizes of the smaller and larger rival and the duration of fighting, it should be possible to distinguish between the two possibilities (Taylor & Elwood 2003; Gammell & Hardy 2003). In both cases, loser RHP will correlate positively with duration. When duration is determined by the loser's RHP, winner size will correlate positively but more weakly with duration. If mutual assessment occurs exclusively, winner size will correlate negatively with duration, but with approximately the same strength as the relationship between loser size and duration (Taylor & Elwood 2003; Gammell & Hardy 2003).

Here, we investigate the question of whether contest duration in the Australian fiddler crab *Uca mjoebergi* is determined by individual thresholds or mutual assessment of fighting ability, and which type of game theory model is most appropriate for this species. We employ the framework for contest analysis suggested by Taylor and Elwood (2003), one of the first studies to do so (see Jennings et al. 2004). In our study species, both males and females occupy and aggressively defend burrows, used as refugia from the high tide and for mating. The surface area around the burrow entrance is used for feeding during diurnal low tides and courtship of wandering females. In fiddler crabs, gravid females select males partly on the basis of burrow characteristics, and remain in the chosen male's burrow while the eggs develop (Backwell & Passmore 1996), and thus ownership of a burrow and surrounding area of the mudflat is important for both survival and reproduction. Burrow-holding males aggressively defend their burrows from wandering males (intruders). An intruder is a male that has lost his burrow, either because he forfeited it to a female whom he mated, or because he lost it in fighting with another male. Intruders wander through the population of territory-holders, and fight with several males before eventually winning a territory. In this study, we artificially create intruders in the population (see Methods for justification), and examine the duration of fights.

Methods

We studied a population of *U. mjoebergi* at East Point Reserve, Darwin, Northern Territory, Australia, from October to December 2003. The study was conducted for 4-6 hours per day during diurnal low tides. Within the areas of the mudflat occupied by *U. mjoebergi*, the population was divided into several smaller sub-populations, separated by unused areas (> 1m in diameter), presumably unsuitable for the construction of burrows (*pers. obs.*). We examined fights between intruders and burrow-holding resident males. There are two ways to do this: either by following naturally occurring wandering males and documenting their fight with a resident; or by artificially creating wanderers by capturing, relocating and releasing resident males and following them until they fight with a resident. We chose the second method because it eliminates several potentially important problems. Firstly, it prevents winner-loser effects since both males were burrow-holders and must therefore have won their last fights (see Hsu & Wolf 1999). Secondly, this method overcomes the possibility that wandering males are a class of weaker individuals that are unable to successfully hold territories (Bradbury & Vehrencamp 1998; Olsson & Shine 2000). Finally, it avoids the possibility of size-assortative fighting if individuals are distributed in a size assortative pattern through the habitat (Christy 1980), as it ensures that males of all sizes could be introduced to each habitat patch.

We captured a burrow-holding male (n = 531) and measured his carapace width and major claw length (pollex and manus) to the nearest 0.1mm using dial callipers, a highly repeatable method (Jennions & Backwell 1996; Backwell & Passmore 1996). All measurements were carried out by a single observer (LJM). We released each male at least 2m away from his own burrow and observed him until he completed his first fight with a resident male defending another burrow. A fight was defined as any interaction in which the males touched claws, even briefly. We recorded the duration of the fight using a stopwatch in seconds (from first to last contact, n = 173 fights), and noted the winner (the male occupying the burrow when the interaction ended). For a subset of the data (n = 109 fights), we also recorded the level of fight escalation. Fights in *U. mjoebergi* escalate from pushing to grappling. Many fights are settled with 'pushing': while facing each other, males align their claws and push. If this does not end an encounter, they proceed to grapple by interlocking claws and twisting (Crane 1975). Once the fight was settled, we captured and measured the male who was originally resident.

We only examined fights between brachychelous (non-regenerated claw) males since regenerated claws have been shown to be inferior weapons (Backwell et al. 2000). We included only those fights in which both males remained on the surface throughout the interaction, and excluded those that involved digging or fighting from within the burrow shaft (n = 173 fights recorded). While males were not marked, we avoided recording the same males in observations on the same day. During each day of observations, we recorded fights in at least two locations on the mudflat (<2m apart), and avoided using the same areas consecutively between days. Thus it is unlikely that the same males or the same dyad were observed repeatedly.

For the analysis of fighting duration, we employ the framework advocated by Taylor and Elwood (2003). We thus investigate winner and loser size as distinct explanatory variables. If, in simple and multiple regression, winner and loser size correlate positively with duration, then duration is determined by individual thresholds. If, however, winner size correlates negatively with duration, with an effect size approximately equal to that of loser size, then mutual size assessment is likely to be occurring, and the two variables can be replaced with a measure of relative size or size difference (Gammell & Hardy 2003; Taylor & Elwood 2003). Taylor and Elwood (2003) also suggest that if mutual assessment has been shown to occur, in a multiple regression involving the size of the loser and a measure of relative size as explanatory variables, only the measure of relative size should be significant. Additionally, we investigate the duration of fights between size matched competitors: mutual assessment predicts that contests between size matched individuals should not vary with the absolute size of the competitors, as their size relative to each other is constant (Enquist & Leimar 1983). If fight duration is based on individual thresholds, fights between two larger size-matched individuals should be longer than those between two smaller size-matched individuals. Encounter duration was log-transformed to normalise the data. All tests are two-tailed and summary statistics are presented as mean ± SE. Analyses were performed using SPSS for Windows, and all reported r^2 are adjusted.

Results

The mean carapace size for crabs was 11.31 ± 0.046mm, and the mean claw size was 17.79 ± 0.124mm (n = 704). Carapace width and claw length were highly correlated (r = 0.958, n = 704, p<0.001), and thus we present here only the results of the analyses for claw size: the results using carapace width are qualitatively similar. There was no difference in mean size between intruders and the residents they chose to fight (residents: 17.82 ± 0.26mm intruders: 17.89 ± 0.24mm, paired t-test: t = 0.269, d.f. = 172, p = 0.788). Fighting was size assortative (correlation between claw size of resident and intruder: r^2 = 0.189, $F_{1,171}$ = 41.167, p<0.001), but with much variation: the ratio of claw sizes (winner claw/loser claw) ranged from 0.741 to 1.852 (mean = 1.153 ± 0.016). To investigate the factors determining the outcome of fights, we followed the approach of Taylor and Jackson (2003) and used three independent predictors of outcome in multiple logistic regression: size of the smaller rival, size of the larger rival, and whether the intruder was larger or smaller than the resident (intruder status). Overall, intruders won 33.4% of fights (exact binomial probability compared to the null expectation of 50%: p<0.001). In multiple logistic regression, the outcome of a fight was predicted by intruder status and the size of the smaller rival (status: B=3.420, d.f.=1, p<0.001, smaller rival size: B=-0.316, d.f.=1, p=0.003). Stepwise multiple logistic regression revealed that only intruder status (larger or smaller) was important in determining outcome (B=3.270, d.f. = 1,

$p<0.001$). In cases where the intruder attacked a larger resident, intruders won only 5.7% of fights, and only the size of the larger (resident) individual was important ($B=-2.673$, d.f.=1, $p=0.049$). Thus, smaller intruders had the best chance of winning when their opponent was not much larger. In cases where the intruder was larger than the resident, intruders won 38.4% of fights. The size of both rivals predicted fight outcome (larger rival: $B=0.552$, d.f.=1, $p=0.002$; smaller rival: $B=-0.689$, d.f.=1, $p<0.001$; overall model: $p<0.001$, Nagelkerke $R^2=0.331$). As the effects are of approximately equal magnitude but opposite direction, the sizes of the larger and smaller rival can be more economically expressed as size difference ($B=0.637$, d.f.=1, $p<0.001$). Overall, both size and residency asymmetries are important in determining the outcome of fights in *U. mjoebergi.* The probability of a fight escalating from the push to the grapple stage was best predicted by the duration of the fight (stepwise logistic regression using smaller rival size, larger rival size, intruder status, fight outcome and fight duration as predictors: duration $B=7.60$, d.f.=1, $p<0.001$). Since many of the aspects of fighting follow patterns well documented in other species, we focus our discussion of fighting behaviour on the factors predicting the duration of fights.

WHAT DETERMINES THE DURATION OF FIGHTS?

The mean duration of fights was 7.48 ± 0.63 seconds (range 0.34 - 71.67 seconds). We began by investigating the relationships between measures of individual size and duration using simple regression. We investigated winner size, loser size and three measures of relative size (winner/loser, winner-loser and (winner-loser)/mean size) as predictors of fight duration (table 2.1). There were significant bivariate relationships between the predictor variables and the duration of fights (table 2.1): all relationships remained significant after correction for table-wide probability using the sequential Bonferroni procedure (Rice 1989, $n = 5$ correlations tested). The strongest single predictor of duration was the size of the loser, and duration correlated positively with both winner and loser size (table 2.1, figure 2.1a and b), and negatively with measures of relative size (table 2.1, figure 2.1c and d).

Following Taylor and Elwood (2003) we compared the size of the winner and loser claw as independent predictors of duration in a stepwise multiple regression model (overall model $r^2 = 0.412$, $F_{2,170} = 61.299$, $p < 0.001$). Both factors remained significant (winner claw: $F_{1,170} = 14.773$, $p < 0.001$, loser claw: $F_{1,170} = 111.234$, $p < 0.001$). The standardised partial regression (β) coefficient for the loser's claw size ($\beta = 0.782$) is positive, while the β coefficient for the winner's size is negative ($\beta = -0.285$), opposite to the simple regression in table 2.1. The results of the multiple regression suggest that duration increases with the size of the loser, and, for a given loser size, duration decreases as the size of the winner increases. However, if mutual assessment only occurs, the effects of winner and loser size in multiple regression are expected to be of opposite direction and approximately equal magnitude (Taylor & Elwood 2003).

Table 2.1: Bivariate regression relationships between claw size variables and duration (log transformed) of fights in *Uca mjoebergi*. All relationships are significant after sequential Bonferroni correction ($n = 5$ tests).

Predictor variable (claw sizes)	r^2	F	n	**sign of slope**	p
loser	0.365	99.658	173	+	<0.001
winner	0.033	6.824	173	+	0.01
winner/loser	0.349	93.030	173	-	<0.001
winner-loser	0.284	69.077	173	-	<0.001
(winner-loser) /mean size	0.333	87.045	173	-	<0.001

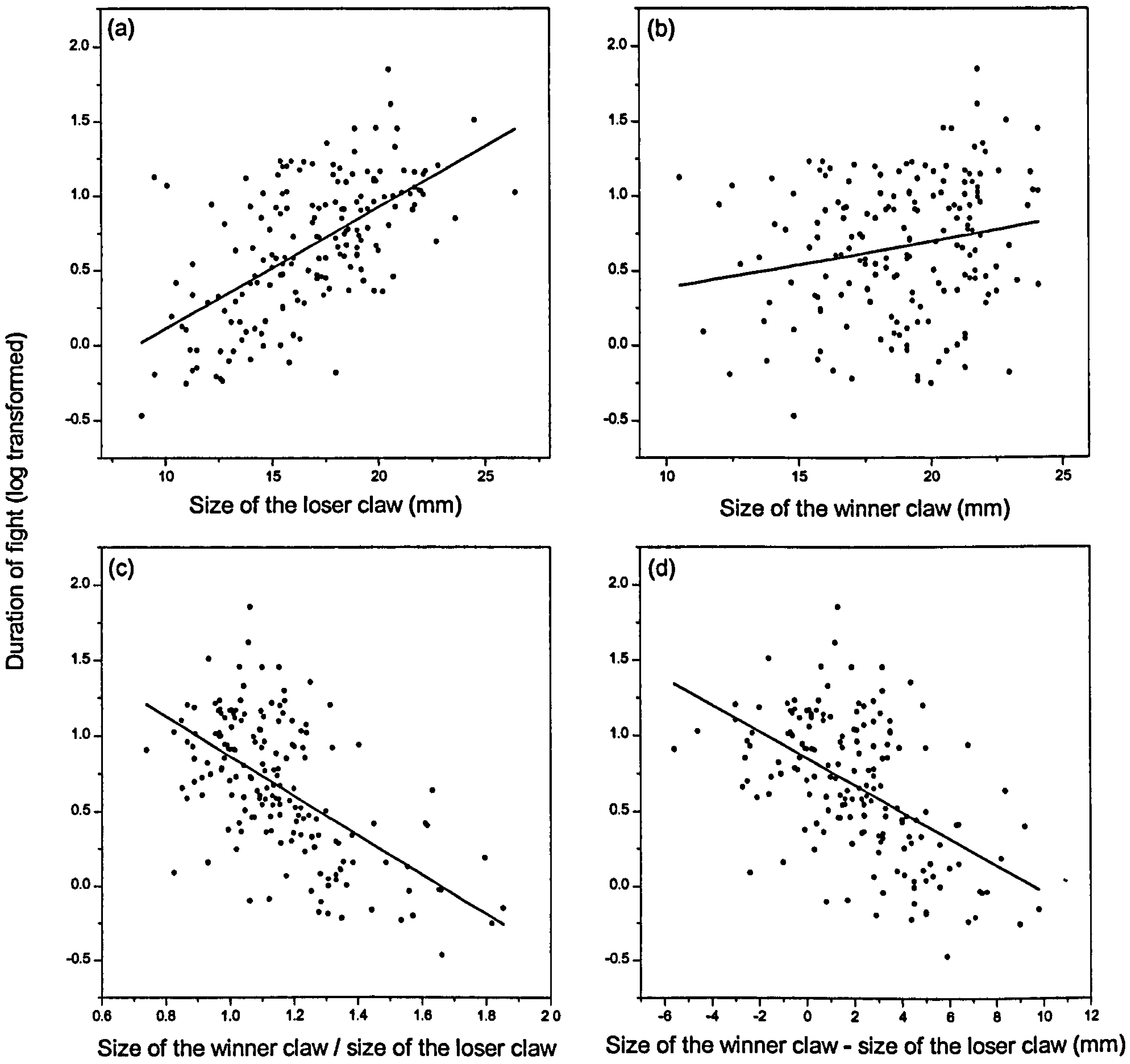


Figure 2.1: Relationship between fight duration in *Uca mjoebergi* and (a) the claw size of the loser, (b) the claw size of the winner (c) the relative claw sizes (winner/loser) and (d) the difference in claw sizes (winner-loser). The regression lines are (a) y = 0.082x - 0.712, (b) y = 0.031x + 0.0725, (c) y = -1.319x + 2.184, (d) y = -0.081x + 0.894 (see the text for full statistical analysis).

The 95% confidence interval for the β coefficient of the winner size (0.139 - 0.431; absolute values) does not overlap with the 95% confidence interval for loser size (0.636 - 0.928), and thus the magnitude of the effects differs at the $\alpha = 0.05$ level, and the size of the loser's claw has a stronger effect on contest duration than the size of the winner's claw. Thus, duration increased most strongly with loser size, and additionally increased as competitors became more size matched. When loser size and a measure of relative size (winner size/loser size) are used as predictors in multiple regression, both factors remain significant (overall model $r^2 = 0.428$, $F_{2,170} = 65.368$, $p < 0.001$, loser claw: $F_{1,170} = 24.773$, $\beta = 0.381$, $p < 0.001$, relative claw size: $F_{1,170} = 20.003$, $\beta = -0.343$, $p < 0.001$). The same is true if size difference (winner size-loser size) is used in place of relative size (overall model $r^2 = 0.412$, $F_{2,170} = 61.229$, $p<0.001$, loser claw: $F_{1,170} = 38.309$, $\beta = 0.445$, $p < 0.001$, size difference: $F_{1,170} = 14.773$, $\beta = -0.277$, $p < 0.001$).

When only fights between closely size matched individuals (0.9 < winner size/loser size < 1.1, $n = 63$ fights) were considered, duration increased with increasing mean size of the competitors ($r^2 = 0.158$, $F_{1,62} = 12.651$, $p = 0.001$, figure 2.2).

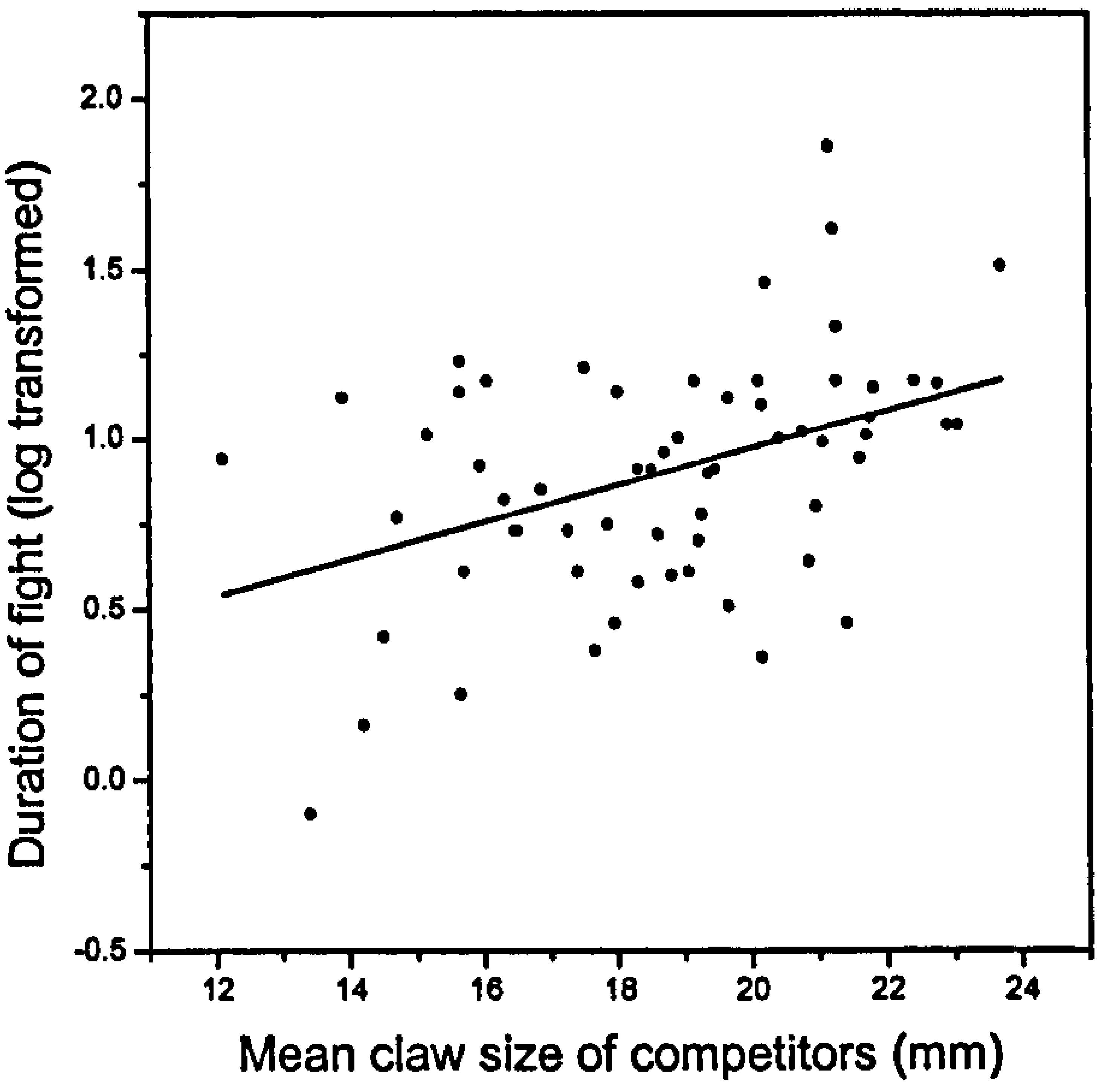


Figure 2.2: Relationship between the mean claw size of two size-matched competitors and the duration of the fight. The regression line is y = 0.054x - 0.107 (see text for statistical analysis).

Discussion

Both the size of the loser and measures of relative size were related to the duration of the fight (figure 2.1). Is the decision of fiddler crabs to retreat in a contest (and lose the fight) based on individual thresholds (own-RHP dependent persistence) or on the assessment of their relative inferiority (mutual assessment)? Our data provide evidence in support of both hypotheses.

Fighting in *U. mjoebergi* is size assortative: intruders tended to fight residents that were of a similar size to themselves, although there was considerable variation. Fights between a very small and a very large individual tended not to occur. This suggests two possibilities. Firstly, small individuals may be able to assess their relative inferiority prior to a fight with much larger individuals, and attempt to avoid the fight by retreating down the burrow (when the resident) or selecting a different opponent (when the intruder). Secondly, large individuals may choose not to challenge residents much smaller than themselves since their burrow may be unsuitably small (Jennions & Backwell 1996). Both possibilities suggest that the decision to begin a fight is based on the assessment of the potential opponent.

The mutual assessment hypothesis is also supported by the finding that winner and loser size had opposing effects in multiple regression. Duration increased with increasing size of the loser but decreased with increasing winner size for a given size of loser. As winners tended to be larger than losers, this implies that duration increases as the size of the winner approached that of the loser, i.e. as the competitors became more closely size matched, or the smaller individual won the fight. More closely size matched individual fought for longer than pairs in which there was a large size discrepancy (figure 2.1c and d).

Taylor and Elwood (2003) predict that if only mutual assessment is occurring, the effect sizes of winner and loser size in multiple regression would be of approximately equal magnitude and opposite direction. However, we found that loser size had a significantly stronger effect on duration than winner size. This suggests that loser size has the greater influence on fighting duration, and that individual thresholds may be important in determining the duration for which an individual is willing to fight. Loser size was also the single best predictor of contest duration (table 2.1, figure 2.1a), and winner size correlated positively with duration (figure 2.1b). Additionally, both loser size and measures of relative size remained significant predictors of duration in multiple regression.

Further support for the hypothesis that fight duration is determined by individual thresholds is seen when fights occurred between closely size-matched individuals. In this situation, fight duration increased with increasing mean size of the competitors, suggesting that larger individuals are able to fight for longer than smaller ones. Models based on relative size assessment (e.g. the sequential assessment game, Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990) predict that the duration of fights between size-matched individuals should be constant regardless of the size of the competitors, since their relative size to each other is constant. Increasing duration with increasing size of size-matched competitors has been noted before (e.g. Dixon & Cade 1986; Glass & Huntingford 1988; Jennions & Backwell 1996; Whitehouse 1997; Taylor et al. 2001), but the implications of this for the applicability of models of fighting behaviour may not have always been recognised (Taylor & Elwood 2003).

Which models of animal contests provide the most appropriate description of fighting behaviour in this particular system? Our results provide partial support for both the own-RHP dependent persistence hypothesis and the mutual assessment hypothesis, but also provide evidence against these hypotheses. Size assortative fighting and opposite effects of winner and loser size provide support for models based on mutual assessment, such as the war of attrition (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982) and sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990), but not for models based on individual thresholds (Mesterton-Gibbons et al. 1996; Payne & Pagel 1996, 1997; Payne 1998). Increasing duration with increasing mean size of size-matched rivals and a stronger effect of loser size suggest the importance of individual thresholds and support models based on own-RHP dependent persistence, such as the war of attrition without assessment (Mesterton-Gibbons et al. 1996) and the energetic war of attrition (Payne & Pagel 1996, 1997; Payne 1998), but not models based on mutual assessment (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982 Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990).

SIZE-ASSORTATIVE FIGHTING?

How can we reconcile these differences? Firstly, can the observed size-assortative fighting explain the differences we see between the predictions of Taylor and

Elwood (2003) and the findings of the current study? In order to investigate this effect on the duration of contests, we provide a modification to the Taylor and Elwood (2003) model, where we consider size-assortative fighting. Following Taylor and Elwood (2003), we consider an animal population in which size is normally distributed about a mean ± SD of 30 ± 6mm. We set up 150 random pairings, and select only those where the ratio of the sizes of the two individuals lies between 0.7 and 1.3, to simulate size-assortative fighting (n = 121 fights). As in Taylor and Elwood (2003), where fight duration is based on individual thresholds, persistence times are randomly dispersed to an approximately normal distribution centred on duration equal to own size with a standard deviation of 5 seconds. Where mutual assessment occurs, and size difference determines duration, duration is equal to 30 seconds minus the absolute size difference between the contestants, randomly dispersed to a normal distribution with a standard deviation of 5 seconds. We found that when duration is determined by individual thresholds, duration of size assortative fights is positively related to winner and loser size in multiple regression (overall model $r^2 = 0.563$, $F_{2,118} = 78.368$, $p<0.001$, winner size: $F_{1,118} = 53.000$, $\beta = 0.523$, $p < 0.001$, loser size: $F_{1,118} = 21.139$, $\beta = 0.330$, $p < 0.001$). When duration is determined by size difference (i.e. mutual assessment operates), duration is positively related to loser size, but negatively related to winner size (overall model $r^2 = 0.281$, $F_{2,118} = 24.423$, $p<0.001$, larger individual size: $F_{1,118} = 47.290$, $\beta = -0.847$, $p < 0.001$, smaller individual size: $F_{1,118} = 37.599$, $\beta = 0.755$, $p < 0.001$). Comparison of the absolute values of the 95% confidence intervals of the β coefficients (larger size: 0.6047 - 1.0893, smaller size: 0.5127 - 0.9973), shows that the effect sizes of the larger and smaller individuals on the duration of contests are of equal magnitude, as in the original Taylor and Elwood (2003) model. Thus, size-assortative fighting alone cannot explain the patterns seen in *U. mjoebergi*, whether mutual assessment or individual thresholds decides the duration of fights.

CUMULATIVE ASSESSMENT?

A potential solution can be found in the cumulative assessment game (Payne 1998). This game resembles the individual threshold models, in that each individual has a threshold level of costs it is willing to bear before retreating in a contest, and costs accrue as the result of the actions of the rival. However, superior rivals (of higher RHP) may inflict higher costs, and/or costs may accrue faster for weaker rivals (Payne 1998, Taylor & Elwood 2003; Briffa et al. 2003). To investigate such effects on the duration of contests, we provide a further extension to the Taylor and Elwood (2003) model, in which fighting is size-assortative, and persistence is based on individual, size-determined, costs thresholds, but larger rivals inflict costs at a higher rate.

In our second modification of the Taylor and Elwood (2003) approach, size is again normally distributed about a mean ± SD of 30 ± 6mm, and we again select only those fights where the ratio of the sizes of the two individuals lies between 0.7 and 1.3 (n = 119 fights). Each rival is willing to accumulate a level of costs proportional to its size, but we incorporate random variation in the relationship between size and cost threshold (expressed as the number of seconds it is willing to fight for) such that thresholds are randomly dispersed to an approximately normal distribution centred on size with a standard deviation of 3 seconds. Opponents inflict costs at a rate proportional to their size: larger individuals inflict costs more rapidly. The duration persistence of an individual is defined as (own cost threshold -   * size of opponent). A fight between two individuals continues until the lower of the two persistence levels has been reached, and this individual is designated the loser. Investigation of the simulated population using simple regression (table 2.2, figure 2.3) reveals similar patterns of relationships to that obtained from our study of fighting in fiddler crabs (table 2.1, figure 2.1). Duration increases with the size of both the winner and the loser, and decreases as the difference in size between the opponents increases. We compared winner and loser size as predictors in stepwise multiple regression (overall model $r^2 = 0.554$, $F_{2,116} = 61.229$, $p < 0.001$), and both factors remained significant (winner size: $F_{1,116} = 7.498$, $p = 0.007$, loser size: $F_{1,116} = 118.033$, $p < 0.001$). As we found in *U. mjoebergi*, the standardised partial regression coefficient for the loser size ($\beta = 0.871$) is positive, while the β coefficient for the winner size is negative ($\beta = -0.219$). The absolute values for the 95% confidence intervals for the β coefficients do not overlap (loser size: 0.712 - 1.030, winner size: 0.060 - 0.378), and thus the magnitude of the effects differs at the $\alpha = 0.05$ level, and loser size in this simulation has a stronger effect on contest duration than the winner size, as it did in our empirical results.

Table 2.2: Bivariate regression relationships between size variables and duration in a simulated population of individuals, where the duration for which an individual is willing to fight depends on individual thresholds, but costs are inflicted more quickly by larger rivals. All relationships are significant after sequential Bonferroni correction ($n = 5$ tests)

Predictor variable (size)	r^2	F	n	**sign of slope**	p
Loser	0.529	133.513	119	+	<0.001
Winner	0.107	15.195	119	+	<0.001
winner/loser	0.169	24.983	119	-	<0.001
winner-loser	0.251	40.440	119	-	<0.001
(winner-loser) /mean size	0.244	38.991	119	-	<0.001

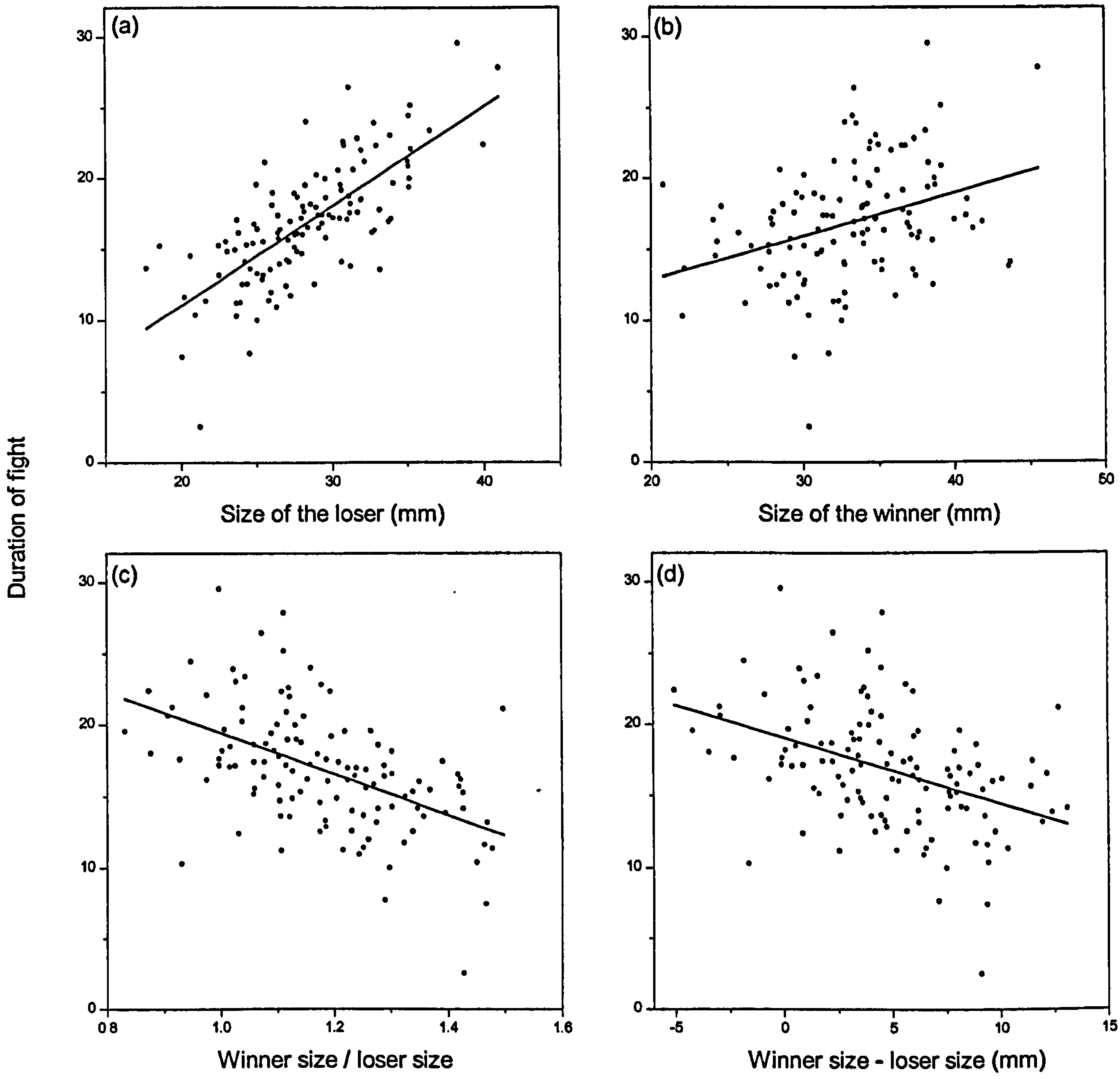


Figure 2.3: In a modification of the Taylor and Elwood (2003) model, individual cost thresholds determine duration, but larger individuals inflict costs more rapidly than smaller ones. When this is the case, in a simulated population, contest duration is predicted by (a) loser size, (b) winner size, (c) relative size (winner/loser) and (d) size difference (winner-loser). The patterns seen are qualitatively similar to those in figure 2.1. The regression lines are (a) $y = 0.703x - 3.055$, (b) $y = 0.306x + 6.759$, (c) $y = -16.58x + 36.651$, (d) $y = -0.57x + 19.59$ (see the text for full statistical analysis).

The simulation provides a reasonable match to the observed data, and suggests that in *U. mjoebergi*, the persistence of individuals in fights is determined by individual thresholds, but that fighting a large opponent causes those thresholds to be reached more quickly, suggesting that no assessment of the opponent need occur. The cumulative assessment game (Payne 1998) may therefore be a more appropriate description of fighting behaviour in this species than the games involving mutual assessment (sequential assessment game: Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990, war of attrition: Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982) or based entirely on individual size (energetic war of attrition, Payne & Pagel 1996, 1997; Payne 1998, war of attrition without assessment, Mesterton-Gibbons et al. 1996). Careful consideration of the dynamics of contests can help distinguish between the true assessment of rival sizes (in the sequential assessment game) and the effect of size on the infliction and accumulation of costs (in the cumulative assessment model, Payne & Pagel 1997; Payne 1998; Briffa & Elwood 2000; Taylor & Elwood 2003), for example, the rate and sequence of actions employed by the contestants within a fight can be studied.

Another possibility is that different assessment mechanisms are used during different phases of the contest. Our data on size assortative fighting suggest some assessment of the opponent occurs before an individual decides to engage in an interaction. It is possible that assessment of opponents may occur during one phase of an escalated fight, while individual thresholds are important in another. To investigate different assessment mechanisms during different phases, data on the duration of the different phases of the fight (e.g the push and grapple phases in fiddler crab fights) would be needed.

Different models may be applicable to fighting behaviour in different species. In sand fiddler crabs, *Uca pugilator*, relative size is a better predictor of contest duration than loser size, providing support for the sequential assessment game (Pratt et al. 2003). In fights for shells in the hermit crab, *Pagurus bernhardus*, stamina and fatigue levels determine the duration and outcome of contests, supporting the energetic war of attrition and the cumulative assessment games (Briffa et al. 1998; Briffa & Elwood 2000). Finally, factors not considered in the original models may also influence fighting behaviour (Pratt et al. 2003), such as the risk of predation (Brick 1999).

Together with recent studies concluding that the duration of fights is determined by individual thresholds (Bridge et al. 2000; Taylor et al. 2001), our result supports the request for reanalysis of much fighting data to take the possibility of individual thresholds into account (Gammell & Hardy 2003). The results of the current and other studies suggest that different models may be appropriate to different species and situations, but the differences between the models need to be tested, and further analysis of the structure of contests may be needed in addition to studies of duration. This is especially true in cases where previous investigation has shown only some support for the model being tested. Alternative models need to be considered where the predictions of only one model have been tested, as data may have been incorrectly interpreted (Gammell & Hardy 2003).

CHAPTER 3

WHY ARE SMALL MALES AGGRESSIVE?

Abstract

Aggression is ubiquitous in the animal kingdom, whenever the interests of individuals conflict. In contests between animals, the larger opponent is often victorious. However, counter-intuitively, an individual that has little chance of winning (generally smaller individuals) sometimes initiates contests. A number of hypotheses have been put forward to explain this behaviour, including the 'desperado effect' according to which the likely losers initiate aggression due to lack of alternative options. An alternative explanation suggested recently is that likely losers attack due to an error in perception: they mistakenly perceive their chances of winning as being greater than they are. We show that explaining the apparently maladaptive aggression initiated by the likely loser can be explained on purely economic grounds, without requiring either the 'desperado effect' or perception errors. Using a game-theoretical model, we show that if smaller individuals can accurately assess their chance of winning, if this chance is less than, but close to, a half, and if resources are scarce (or the contested resource is of relatively low value), they are predicted to be as aggressive as their larger opponents. In addition, when resources are abundant, and small individuals have some chance of winning, they may be more aggressive than their larger opponents, as it may benefit larger individuals to avoid the costs of fighting and seek alternative uncontested resources.

Introduction

Aggression is ubiquitous in the animal kingdom, occurring whenever the interests of individuals conflict (Huntingford & Turner 1987). It has been shown that differences in resource holding potential (RHP; Parker 1974) play an important role in determining the outcome of contests (Maynard Smith & Parker 1976; Maynard Smith 1982; Enquist & Leimar 1983; Beaugrand et al. 1996; Jennions & Backwell 1996 Petersen & Hardy 1996; Alcock & Bailey 1997; Chellappa et al. 1999). Individuals may assess their RHP relative to that of their opponent before making a decision as to how to proceed in a contest, and low RHP individuals may avoid costly competition with superior rivals by assessing their relative inferiority and retreating (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Enquist & Leimar 1983). Larger individuals are likely to win an escalated contest whereas smaller ones are unlikely to obtain the disputed resource in such a contest, and often pay a cost associated with fighting (Parker 1974). Although there are many examples of larger individuals acting aggressively towards smaller ones (e.g. Zack 1975; Brace & Pavey 1978; Dowds & Elwood 1983; Figler & Einhorn 1983; Barlow et al. 1986; Turner & Huntingford 1986; Lindström 1992; Keeley & Grant 1993; Thorpe et al. 1994), there are also cases where aggression is predominantly initiated by the smaller competitors (Dow et al. 1976; Enquist & Jakobsson 1986; Ribowski & Franck 1993; Smith et al. 1994; Morris et al. 1995; Moretz 2003). As one would expect small individuals to be the likely losers, this behaviour may seem irrational and therefore the evolution of such a 'Napoleon complex' (Just & Morris 2003) is intriguing.

There are several possible explanations for why small individuals may initiate fights or act aggressively towards larger individuals. Firstly, small individuals may perceive themselves as being of higher RHP or larger size than their opponent and initiate escalation by mistake (Bradbury & Vehrencamp 1998), or they may not be able to assess relative size prior to an interaction if such information is only obtained through display (Smith et al. 1994). Secondly, small individuals may value the resource item more highly than larger individuals, that is, there is a resource value asymmetry between the contestants, known to influence the outcome of fights (e.g. Davies & Houston 1981; Shutler & Weatherhead 1992; Eason & Hannon 1994; Johnsson et al. 2000; Johnsson & Forser 2002). For instance, in pumpkinseed sunfish *Lepomis gibbosus* when probable losers were provided with more food (increasing the expected value of the resource), they became more likely to attack (Dugatkin & Olsen 1990). Thirdly, small individuals may attack because this increases the probability that they win the fight. Conflict outcome in favour of the initiator has been observed in a number of species (Jackson 1991; Figler et al. 1995; Hack 1997; Martin et al. 1997; Taylor et al. 2001; Roeder et al. 2002). Finally, small individuals may attack because they have few alternative opportunities to obtain resources (the 'desperado effect'; Grafen 1987). Grafen (1987) pointed out that any convention that leaves a group of individuals unable to gain access to a resource cannot be evolutionarily stable, since members of the excluded group have nothing to lose by ignoring the convention. Thus, if smaller individuals were to always retreat from a resource when they found it contested by a larger individual, they would never be able to obtain such resources, and so aggression by small individuals might be predicted.

Most theoretical models of animal contests, such as the sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984), do not predict which individual should initiate an escalated contest: escalation is assumed to occur simultaneously. Hurd and Enquist (1998) predicted that weaker individuals should attack larger opponents when they have few alternative options, and they are unaware of their opponent's strength. Otherwise, weaker individuals are predicted to retreat, leaving the stronger to claim the resource. However, Hurd and Enquist (1998) assumed that the stronger individual would always be victorious in a contest. Mesterton-Gibbons (1994) investigated the effect of variation in RHP on aggression, and found that under certain limited conditions, a low RHP individual could be expected to become involved in an escalated contest with a higher RHP opponent, but only when the difference in RHP was small. Hurd and Enquist (1998) and Mesterton-Gibbons (1994) predict equal levels of aggression from low and high RHP individuals despite asymmetries in RHP, but do not predict that low RHP individuals should be more aggressive than their opponents of higher RHP.

Although body size has been found to be a good surrogate measure of RHP (e.g. Morris et al. 1995; Jennions & Backwell 1996), the larger individual may not always be successful in a contest. In some cases, smaller individuals may win, as other factors may contribute to fighting ability (e.g. Marden & Waage 1990; Alcock & Bailey 1997; Brick 1999; Hofmann & Schildberger 2001). In an investigation of ownership priority as a convention for settling disputes (bourgeois behaviour) in the hawk-dove game, Eshel and Sansone (2001) found that ownership priority is replaced by strength priority (i.e. weak individuals give way to stronger ones) when the availability of territories and the costs of fighting decreases. However, when resources are scarce and non-owners suffer from a high death rate, smaller individuals are predicted to attack opponents that are not much larger than themselves. Where one individual is already resident at a resource, stronger individuals are likely to accumulate as owners (since they have a higher probability of winning a contest), leaving the weaker individuals as floaters. Both respect for ownership and respect for strength would leave these individuals in a desperado position (Grafen 1987).

Investigating the question of why small males initiate escalation in fights in the absence of resource value or ownership asymmetries, Just and Morris (2003) developed a model where individuals estimate their probability of winning a fight, based on the difference in RHP between them. They found that if there is error in this estimation, then likely losers may perceive themselves to be likely winners, and initiate escalation, while likely winners may not always attack first. But is it necessary to invoke perception errors as an explanation for aggression directed from small to large individuals, or is limited resource availability (Grafen 1987) enough to cause small individuals to initiate fights that they are likely to lose? We investigate the aggressive behaviour of individuals differing in RHP when there is no complicating residency asymmetry (for example, contests over food resources rather than territories), and ask whether aggression should be initiated by the small or large contestant, when both competitors are aware of their own and their opponent's fighting ability, but when body size (or RHP) does not perfectly determine fighting outcome.

Model

Two individuals that differ in size compete for access to a resource. Each individual can choose one of three behavioural options: it can attack the other (A), display while waiting for its opponent to attack, and then retaliate (W), or retreat from the conflict (R). Throughout, capital letters (A, W, R) refer to the behavioural choice of the larger individual and lower-case letters (a, w, r) to the behavioural choice of the smaller individual. In a bimatrix game, where the payoffs to the opponents differ due to differences in their RHP, and both competitors are aware of their own and their opponent's RHP, mixed strategies cannot be evolutionarily stable (Selten 1980; Crowley 2000), and thus we restrict our analysis to pure strategies.

The smaller individual has a probability p of winning a contest where both individuals choose the same behavioural option (i.e. both decide to attack or wait). We assume that the first to initiate aggression gains an advantage in the fight (e.g. Figler et al. 1995). Where the smaller individual chooses to attack, and the larger individual chooses to wait, the probability of the smaller individual winning increases by α. Likewise, when the smaller individual chooses to wait, and the larger individual chooses to attack, the probability that the smaller individual wins the fight decreases by α. The parameters of the model can be found in table 3.1.

The individuals contest a resource of value V. If one individual chooses to attack, and the other to display, the displaying individual will retaliate, and a fight will occur. A fight also occurs if both individuals choose to attack. In either case, both individuals pay a cost c_f. If both choose to wait/display, they pay a cost c_d. The cost of displaying (c_d) is lower than that of fighting (c_f). If one individual chooses to attack while the other chooses to retreat (i.e. the smaller individual chooses a and the larger individual chooses R, or the smaller individual chooses r and the larger individual chooses A), the retreating individual pays a cost β, and the attacking individual pays a cost γ. Both costs β and γ are less than the cost paid if a fight occurs (c_f). If one individual retreats, the other gains full access to the resource, and can claim the benefits V. If one or both individuals retreat, they have a probability F ($F<1$) of finding an uncontested resource. This effectively reduces the value of the contested resource: the relative resource value is defined as $V-FV$.

Table 3.1: Parameters and variables

Parameter	Description
A (a)	Strategy of high (low) RHP individual is to attack
R (r)	Strategy of high (low) RHP individual is to retreat
W (w)	Strategy of high (low) RHP individual is to display
p	Probability that the smaller individual wins a contest
α	Increase in winning probability for the first to attack
c_f	Cost of fighting (for either contestant)
c_d	Cost of displaying
V	Value of a resource item
F	Probability of finding an uncontested resource
β	Cost of being attacked while retreating
γ	Cost of attacking a fleeing opponent

Table 3.2 outlines the payoff matrix for the contest for the smaller (3.2a) and larger (3.2b) individuals, for each potential combination of behavioural options. The fitness of an individual is calculated from the total payoff it receives, which depends on the behavioural choice of that individual, and the behavioural choice of the opponent. For example, if both individuals choose to attack (a and A), the payoff to the smaller individual is $pV-c_f$, and the payoff to the larger individual is $(1-p)V-c_f$.

Table 3.2: Payoffs to (a) the smaller individual and (b) the larger individual in an interaction, dependent on their respective behaviours.

		Strategy choice of the larger individual		
		A	W	R
(a) Strategy choice of the smaller individual	a	$pV-c_f$	$(p+\alpha)V-c_f$	$V-\gamma$
	w	$(p-\alpha)V-c_f$	$pV-c_d$	V
	r	$FV-\beta$	FV	FV
(b) Strategy choice of the smaller individual	a	$(1-p)V-c_f$	$[1-(p+\alpha)]V-c_f$	$FV-\beta$
	w	$[1-(p-\alpha)]V-c_f$	$(1-p)V-c_d$	FV
	r	$V-\gamma$	V	FV

We derive the best replies to the strategy of the opponent in the following way, and summarise these in table 3.3: If the larger individual chooses to attack (*A*), the small individual should reply by attacking (*a*) if the payoff from doing so is greater than the payoff from either displaying (*w*) or retreating (*r*). Thus, *a* is a best response to *A* if:

$$pV - c_f > (p-\alpha)V - c_f \tag{1}$$

and

$$pV - c_f > FV - \beta \tag{2}$$

Inequality (1) is satisfied whenever $\alpha > 0$, that is, whenever there is an advantage to initiating aggression, which is assumed to be true, and inequality (2) is satisfied when:

$$F < p - \frac{c_f - \beta}{V} \tag{3}$$

Displaying (*w*) is the best response to *A* when it pays more than *a* or *r*, which occurs when inequality (1) is not satisfied, and when:

$$(p-\alpha)V - c_f > FV - \beta \tag{4}$$

which is satisfied when:

$$F < (p-\alpha) - \frac{c_f - \beta}{V} \tag{5}$$

As α is always positive, inequality (1) is always satisfied, and thus *w* is never a best response to *A*. Retreating (*r*) is the best response to *A* when it pays more than *a* or *w*, which occurs when inequalities (3) and (5) are both not satisfied. By observation, this only requires that inequality (3) is not satisfied. The conditions for the best responses to *A*, *W*, *R*, *a*, *w* and *r* are summarised in table 3.3.

Table 3.3: Conditions and responses to all opponent strategies.

Opponent strategy	Response	Conditions
A	a	$F < p - \frac{c_f - \beta}{V}$ (3)
	w	Never
	r	$F > p - \frac{c_f - \beta}{V}$ (6)
W	a	$\alpha > \frac{c_f - c_d}{V}$ (7) and $F < p + \alpha - \frac{c_f}{V}$ (8)
	w	$\alpha < \frac{c_f - c_d}{V}$ (9) and $F < p - \frac{c_d}{V}$ (10)
	r	$F > p + \alpha - \frac{c_f}{V}$ (11) and $F > p - \frac{c_d}{V}$ (12)
R	a	Never
	w	Always, as $\gamma > 0$ and $F < 1$
	r	Never
a	A	$F < (1-p) - \frac{c_f - \beta}{V}$ (13)
	W	Never
	R	$F > (1-p) - \frac{c_f - \beta}{V}$ (14)
w	A	$\alpha > \frac{c_f - c_d}{V}$ (7) and $F < 1 - (p - \alpha) - \frac{c_f}{V}$ (15)
	W	$\alpha < \frac{c_f - c_d}{V}$ (9) and $F < (1-p) - \frac{c_d}{V}$ (16)
	R	$F > 1 - (p - \alpha) - \frac{c_f}{V}$ (17) and $F > (1-p) - \frac{c_d}{V}$ (18)
r	A	Never
	W	Always, as $\gamma > 0$ and $F < 1$
	R	Never

We can now proceed to specify which combinations of pure strategies are candidate ESSs, and the conditions under which these can occur.

1. Both attack (A-a)

Both individuals should attack when inequalities (3) and (13) are satisfied; by observation, satisfying equation (3) guarantees satisfaction of (13).

2. Both display (W-w)

Both individuals should choose to display if inequalities (9), (10) and (16) are satisfied.

3. Both Retreat (R-r)

Both individuals retreating can never be an ESS, since retreating is never the best response to a retreating opponent.

4. Attack-display (A-w) and Display-attack (W-a)

Attack-display and Display-attack can never be ESSs because waiting is never the best response to an attacking opponent, because the payoff from attacking an attacking opponent is always greater than the payoff from displaying to an attacking opponent (tables 3.2 and 3.3)..

5. Retreat-attack (R-a) and Attack-retreat (A-r)

Retreat-attack and Attack-retreat can never be ESSs, since the cost of attacking a retreating opponent means that it is always better to display to it.

6. Retreat-display (R-w)

The larger individual should choose to retreat (R) and the smaller individual should display (w) when inequalities (17) and (18) are satisfied.

7. Display-retreat (W-r)

The smaller individual should choose to retreat (r) and the larger individual should display (W) when inequalities (11) and (12) are satisfied.

It is clear by inspection that *W-w* cannot coexist with *W-r* or *R-w*. It is also clear that *W-w* and *A-a* can coexist as ESSs, when the conditions for both are met. *A-a* can coexist with *W-r* when: $p-\frac{c_f-\beta}{V}>p+\alpha-\frac{c_f}{V}$, which occurs when $\alpha V<\beta$ (when the additional benefits gained by attacking first are less than the costs associated with being attacked while retreating), and the conditions necessary for both are satisfied. *A-a* can also coexist with *R-w* when equations (17), (18), and (3) are all satisfied. *R-w* and *W-r* can coexist as ESSs when all the conditions for their occurrence are met (equations 11, 12, 17 and 18). By inspection, given that $p<0.5$, the value of F needed to satisfy equation (18) is greater than the value needed to satisfy equation (12). Thus, *W-r* and *R-w* will coexist when the conditions for *R-w* are satisfied, but *W-r* will also exist in parameter space where *R-w* does not.

Results

A 'Napoleon ESS', where the model predicts that the smaller individual is more aggressive than the larger one, occurs where the smaller individual displays and the larger individual retreats (*R-w*), illustrating greater aggression by the smaller individual. This occurs when the probability of finding an uncontested resource is high (larger values of F) and the probability that the smaller individual wins is low (small p), and always coexists with an alternative ESS, where the larger individual displays and the smaller individual retreats (figure 3.1). This ESS is not particularly sensitive to the costs of fighting (c_f, figure 3.2). The alternative ESS (*W-r*) also exists over a much wider range of the parameter space (figures 3.1 and 3.2), and is the predominant solution to the game when RHP accurately determines the outcome of fights ($p = 0$).

The model predicts equal levels of aggression by both individuals (*A-a*) when the probability that the smaller individual wins is high (values of p approaching 0.5) and the contested resource is of relatively low value (low $V\text{-}FV$, high values of F; figure 3.1). This also occurs when the costs associated with fighting are low (low c_f, figure 3.2). This ESS can coexist with an ESS where both individuals choose to display while waiting for their opponent to attack (figure 3.1a). If, however, $\alpha > \frac{c_f - c_d}{V}$, that is, the advantage gained by initiating aggression exceeds the relative difference in the costs of the two fight types (fighting and displaying), the *W-w* ESS does not coexist with *A-a* (figure 3.1b). In this case, an area of parameter space exists where there is no ESS, when $\beta < \alpha V$ (when the cost of being attacked while retreating is less that the possible gains from attacking first).

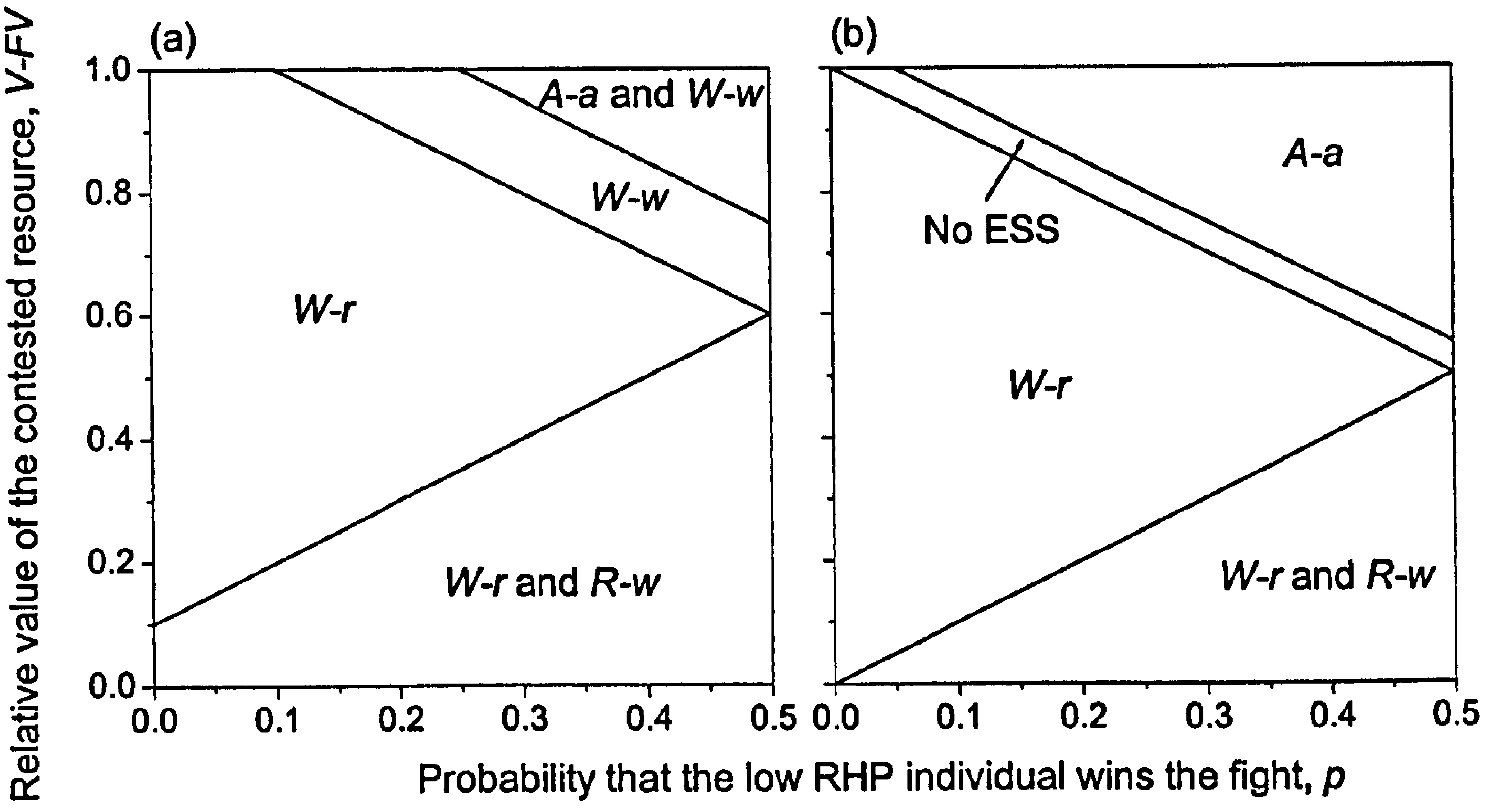


Figure 3.1: Effect of increasing the probability that the smaller individual wins the fight (p), and relative value of the contested resource (V-FV) on the ESS solutions of the game. Parameter values used a) α=0.1, c_f=0.3, c_d=0.1, β=0.05, V=1, b) α=0.1, c_f=0.1, c_d=0.1, β=0.05, V=1.

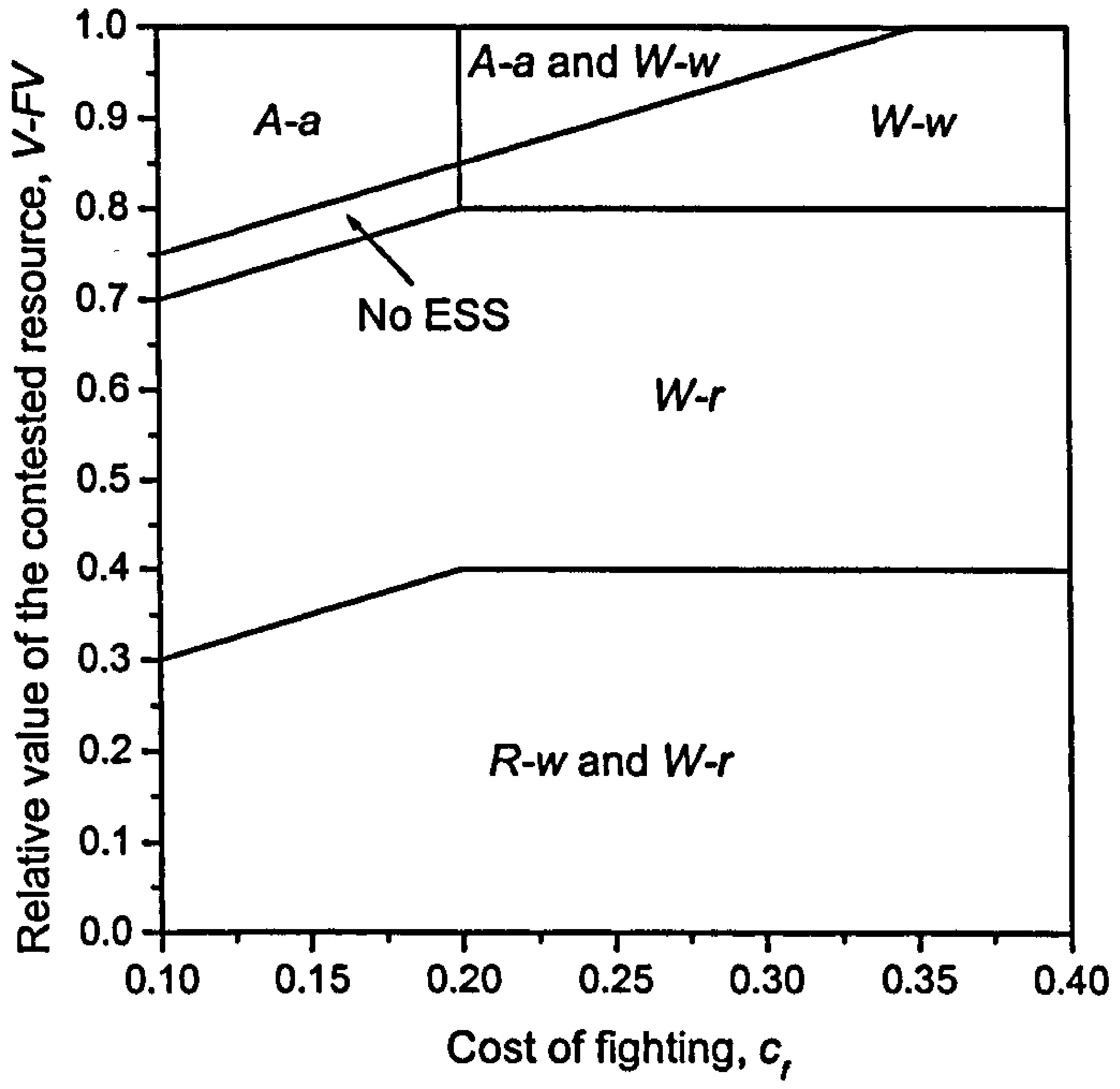


Figure 3.2: Effect of increasing the cost of fighting (c_f) and the relative value of the contested resource (*V-FV*) on the ESS solutions of the game. Parameter values used: α=0.1, p=0.3, c_d=0.1, β=0.05, V=1

To investigate the behaviour of the individuals within the area of parameter space where there is no ESS, we performed simulations of the responses of one larger and one smaller individual to the behaviour of their opponent. We began by randomly selecting a strategy for each individual (*A*, *W* or *R* for the larger individual, *a*, *w* or *r* for the smaller individual). In each time step, each individual is free to respond optimally to the behaviour of the other, and we calculate the payoff each individual could gain from each response using the payoff matrices in table 3.2. For example, if the larger individual first chooses to attack, the potential payoffs to the smaller individual are found in the first column of table 3.2a. Each individual selects the behaviour giving the highest payoff to use in the next time step. We assume that the individuals respond simultaneously to their opponent's behaviour in the previous time step, for *t* time steps. Preliminary simulations covering all the parameter space showed that where the analytical model predicted ESSs, they were reached quickly. Running the model for extended populations had no effect on the ESSs emerging from the simulation.

In the area of parameter space where no ESS was predicted, a pattern of cycling between strategies by each individual occurred, illustrated in figure 3.3. If we begin by assuming that both individuals attack (*A-a*, marked by a circle in figure 3.3), the best response of the smaller individual is to retreat, to which the best response of the larger individual is to attack. In the next step, the strategy set is therefore *A-r*. The best response of a larger individual to a retreating opponent is to wait/display, and the best response of the low-RHP individual to an attacking opponent is to retreat, thus, the strategy set in the next step is *W-r*. Given the parameter values, the best response of the larger individual is to continue waiting, and the best response of the smaller individual is to attack (*W-a*). The cycle is completed as the best response to this is for both individuals to attack (*A-a*).

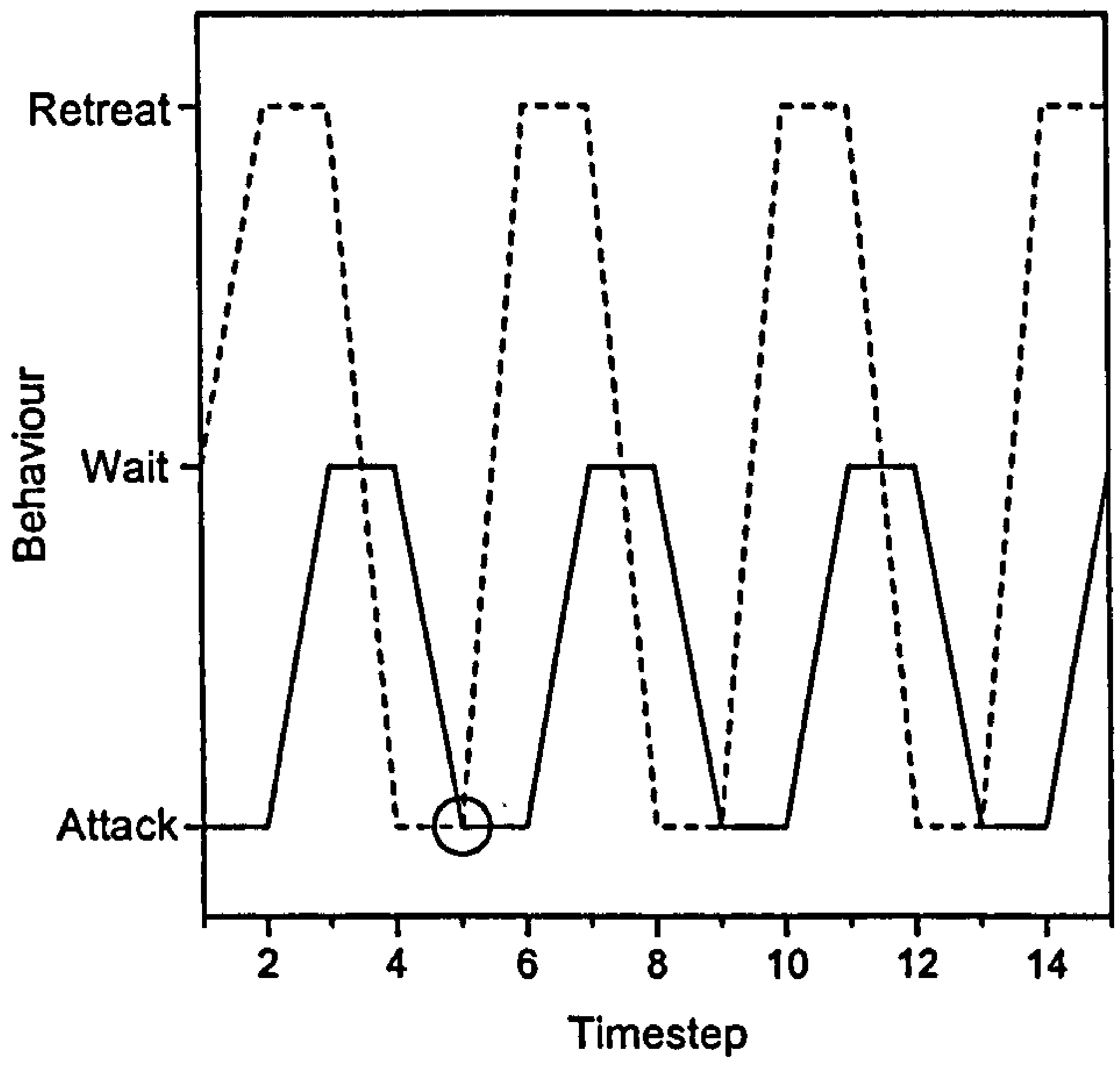


Figure 3.3: Patterns of cycling between strategies in the area of parameter space where there is no ESS. Solid line: choice of larger individual, dashed line: choice of smaller individual. Parameter values used: p=0.3, F=0.25, α=0.1, c_f=0.1, c_d=0.1, β=0.05, V=1. Circle marks the start of the cycling pattern described in the text, after the cycling has stabilised from random starting strategies for both individuals

Discussion

Both attacking (*A*, *a*) and displaying (*W*, *w*) can be considered to be aggressive behaviours. Displaying represents a low level of aggression, and attacking a high level, as it results in an escalated fight. Only retreating is considered to be a non-aggressive strategy in the current model. Thus, smaller individuals can be said to be aggressive when they select an attack (*a*) or display (*w*) strategy. Our model predicts a Napoleon ESS, where the Napoleon strategy is defined as meaning that smaller individuals are more aggressive than their larger opponents, when smaller individuals display and larger ones retreat. This occurs when the smaller individual has some chance of winning a contest (values of p approaching 0.5), and resources are abundant and of relatively low value (large values of F, resulting in low values for $V-FV$). Thus, when resources are freely available, and contests are not always resolved in the favour of the larger individual, it can benefit the larger individual to retreat. A possible example of this behaviour may occur in natural populations of snow buntings (*Plectrophenax nivalis*) where older males retreat in response to aggression over food resources from younger males (Smith & Metcalfe 1997). The Napoleon ESS coexists with an alternative, 'common-sense', ESS, where smaller individuals retreat when challenged by a larger individual. When there are few alternative options, and the smaller individual has little chance of winning, this common-sense solution becomes the only ESS.

Smaller individuals attack if resources are scarce and consequently each is of high relative value (low values of F), they have a reasonable chance of winning the fight (p approaching 0.5), and the costs of fighting are low (low c_f). Thus, aggression can be expected from smaller individuals when they have few alternative options, and when RHP (or body size) is not a perfect determinant of fight outcome. This reflects the findings of previous models, where aggression was favoured when individuals have similar RHP (Mesterton-Gibbons 1994), and when individuals gain more by fighting than they would by giving up (Hurd and Enquist 1998). Similarly, Eshel and Sansone (2001) predicted that high levels of aggression could occur in smaller individuals, particularly towards those not much larger than themselves (i.e. where they have some chance of winning in a fight), when resources are scarce.

In our model, high intensity aggression is favoured when resources are scarce and valuable, and fights incur low costs relative to the value of the resource. These cases have both been noted previously. In the hawk-dove game (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Parker & Knowlton 1980), low fight costs are more likely to promote aggression, and the desperado effect (Grafen 1987) predicts the undermining of conventional settlement of disputes when resources are scarce and one class of individuals is left with few or no alternative options. Our model suggests that under the conditions that favour aggression (i.e. low fighting costs and scarce, high value resources), smaller individuals are predicted to attack even when they can accurately assess their chances of winning in a fight, so long as body size is not a completely accurate predictor of fight outcome. Smaller individuals do not need to consider themselves to be likely to win in order to act aggressively, as proposed by Just and Morris (2003). Such an outcome has been observed, for instance, in the cichlid fish *Aequidens rivulatus*, where behavioural signals indicating which individual is likely to win appear to be perceived accurately, and yet escalated fighting is still observed (Maan et al. 2001).

We found no situations where the smaller individual chose an attacking strategy (a) and the larger individual chose to display (W). This occurs because the non-attacking individual can always improve its fitness by attacking back (see methods), as we assume that a fight always occurs if one competitor chooses to escalate. We assume that the costs of fighting are equal for both competitors, but extending the model to incorporate asymmetries in the costs between competitors or fight outcomes may provide a wider range of potential ESSs. For example, smaller individuals may pay higher costs of fighting (Maan et al. 2001), or losing may be more costly than winning (Chellappa & Huntingford 1989; Neat et al. 1998), or display intensity may be an honest signal of RHP and thus more costly to a high RHP individual (Zahavi 1975, 1977). Although for simplicity we assumed that costs (c_f, c_d, β and γ) are identical for the two competitors, our results are not critically dependent on this assumption. If the cost of fighting for either individual was unilaterally increased, we would expect that their, but not their opponent's, enthusiasm for aggression to decrease, leading to a greater area of parameter space where the individuals do not behave identically, but retaining areas of aggression by both.

We assume that the first individual to attack has an advantage, described by α. As this is additive, we implicitly assume that the mechanism providing this advantage is unrelated to RHP. For example, the advantage may be due to the element of surprise, and the use that can be made of that surprise (for example, landing a blow on an unsuspecting opponent) is independent of the qualities that govern victory in more symmetric contests (i.e. is independent of RHP, and equal for both competitors). However, there may be other biological situations where the advantage is more closely related to RHP, and in this case it would be more appropriate to assume a multiplicative rather than additive increment. The consequence for the model would be that the absolute benefits of attacking are greater for the larger individual, and we would therefore expect to see lower levels of aggression by the smaller individual. We would not, however, see a complete lack of aggression by smaller individuals, particularly when resources are scarce and valuable.

Studies of fighting behaviour tend to focus only on the interactions that have occurred, and do not report cases where one individual has retreated without a fight (e.g. Hu & Morse 2004). This makes it difficult to explain why escalated fights occur. However, escalated encounters have been reported when individuals are closely size matched (e.g. Ribowski & Franck 1993, Smith et al. 1994; Morris et al. 1995), suggesting that the smaller individual has some chance of winning in fights (high *p*, close to 0.5). Where there are large differences in body size, aggression often does not occur, and the smaller individual retreats from the larger (e.g. Smith et al 1994), presumably because it assesses its chances of winning as being prohibitively low (small values of *p*).

As escalated fighting is observed much more frequently in experimental systems than in nature (Tinbergen 1968), it has been suggested that the empirical observation that smaller individuals can be aggressive may be an artefact of experimental design. In experiments on fighting, individuals are often placed in artificially symmetrical situations, for example, if residency is confused (Waage 1988), and both contestants consider themselves to own the resource. Escalated fighting occurs in these conditions many times more frequently than when only one of the individuals considers itself owner (reviewed in Kemp & Wiklund 2001). Individuals are also given few alternative options to obtain resources other than fighting. When losers of fights between *A. rivulatus* were able to withdraw from an experimental arena, conflicts were of shorter duration, and escalated fighting was absent, compared to when no alternative options were present (Maan et al. 2001), suggesting that the desperado effect (Grafen 1987) may be a frequent cause of aggression in experimental situations.

In general, there seems to be little evidence for desperado behaviour in natural populations. In red-winged blackbirds (*Agelaius phoeniceus*, Shulter and

Weatherhead 1992), and *Anolis aeneus* lizards (Stamps & Krishnan 1995), the costs of fighting to take over a territory appear to be higher than the costs of waiting for a vacancy, and aggressive territorial take-overs rarely occur. Additionally, naturally occurring fights, where individuals are free to choose opponents, tend to be size assortative: individuals avoid contests with opponents who differ greatly in size (Jennions & Backwell 1996; Pratt et al. 2003), but retreating from an opponent occurs relatively rarely in experiments (Smith et al 1994; Hu & Morse 2004). The desperado effect therefore needs to be ruled out as a cause of aggression in experimental systems before the evolution of aggressive behaviour can be understood (Maan et al. 2001).

CHAPTER 4

ADAPTIVE STRATEGIES OF TERRITORY FORMATION

Abstract

How do territorial animals gain ownership of an area? Early modelling considered the evolution of fighting when the winner can claim the right to the resource. Recently, alternative hypotheses have been offered where repeated interactions lead to division of space through 'nagging' instead of one decisive fight. However, these models assume that animals avoid areas in which they have taken part in aggressive interactions, but do not consider whether avoidance itself is adaptive. We aim to bridge this gap between mechanistic and adaptive explanations, by presenting a game theory model where individuals choose whether to return to an area after a fight with a specific outcome (win, loss, draw). We show that avoidance of areas where fights have occurred can be adaptive, but only if the benefits of access to the area are low compared to the costs of fighting. Otherwise, one individual (typically the winner) responds by returning to the area, and the other (loser) avoids it. In such cases, space is gained by winning fights. We also consider the role of conventions. If responses to fights were purely conventional, paradoxical strategies where losers of fights gain ownership would be equally as logical as common-sense ones where winners claim ownership. Paradoxical solutions can be stable but only when there is little difference in fighting ability between the competitors, when individuals adhere very strictly to a behavioural rule without much random variation, and when the population in its ancient state used a paradoxical strategy.

Introduction

In territorial animals, ownership of a territory is usually a prerequisite to breeding, indicating strong selection pressure to win such resources. How contests over resources are resolved was the first question that brought game theory to the attention of biologists (Maynard Smith 1982). Early modelling concentrated on 'hawk-dove' games (Maynard Smith & Price 1973; Grafen 1979), which assume that only one of the contestants can win the resource. Such games often include an asymmetry between owners, who have been resident before, and intruders, who have not. These models have been modified to include, for example, size differences (Crowley 2000) or repeated interactions (Houston & McNamara 1991). However, existing game theory models of conflict focus on winner-takes-all fights for indivisible space.

Other models of territorial settlement look at the sequential arrival of individuals, such as birds at a nesting area or males at a lek. These models focus on an individual's timing of arrival (Kokko 1999) or whether it should contest an occupied site or settle in a vacant patch (Broom et al. 1997), rather than looking at simultaneous arrival and exploration of vacant space. However, both these types of model are inappropriate for modelling territorial settlement if aggressive interactions lead to the sharing of space between competitors settling in the same area (e.g. juvenile *Anolis aeneus* lizards, Stamps & Krishnan 1995, 1998). In this case, social interactions during territory establishment may resemble bargaining and negotiation, in that both contestants would benefit from sharing a divisible resource rather than risking escalated contests (Maynard Smith 1982).

Consequently, an alternative approach to modelling territory acquisition is advocated by Stamps and Krishnan (1999, 2001). Based on observations of territorial settlement in the lizards (Stamps & Krishnan 1997), they model a situation in which no single interaction determines the winning of an entire indivisible territory. Instead, individuals move through a large, suitable, divisible area and increase the use of sites that appear attractive to them. It is important to note that in these models, all sites within the habitat are of equal intrinsic quality; thus, the attractiveness of an area relates solely to the experiences an individual has within it. Fights involve punishment that reduces the attractiveness of an area for both individuals, while entering an area uncontested increases its attractiveness. Thus, through a tendency to avoid areas in which they have taken part in aggressive interactions, regardless of the outcome, and only returning to areas where positive experiences (increasing familiarity) outweigh negative ones (fights), animals can gain exclusive use of space (Stamps & Krishnan 1999). In these models, the gaining of territorial areas occurs through frequent 'nagging' instead of one decisive fight.

Stamps and Krishnan's (1999, 2001) models reproduce several features of territorial systems (Sih & Mateo 2001), and thus are a clear step forward in developing more realistic models of territory acquisition. However, they differ in one crucial respect from game theory models: they do not evaluate the adaptiveness of the behaviour on which they are based. In particular, one should investigate whether animals benefit from a tendency to avoid areas where they have previously encountered a competitor regardless of the outcome of the encounter, as it is assumed in Stamps and Krishnan (1999, 2001).

Here we develop a new model that addresses these issues, with particular reference to two questions. Firstly, we investigate whether avoidance behaviour is adaptive. In other words, if individuals are given the choice of not returning to an area, or returning less frequently, should they do so (Stamps 1994; Stamps & Krishnan 1999, 2001), or attempt to gain space by winning fights, as dyadic models of territorial contests generally suggest (Maynard Smith & Parker 1976)? Secondly, we ask why respect for ownership can become established in territorial systems. Early game theory models (e.g. Maynard Smith & Parker 1976; Maynard Smith 1982) suggest that 'paradoxical' solutions to animal conflict — where, for example, owners, or individuals of high resource holding potential (RHP) simply retreat when challenged — can theoretically be as reasonable as the common-sense solutions, in which high RHP individuals or owners are more willing to fight than intruders. A paradoxical evolutionary stable strategy (ESS) is thus an evolved behavioural convention dictating that an individual of lower RHP, or less to gain from winning a contest (depending on the asymmetry under consideration), obtains access to a disputed resource at the expense of a more able or motivated contender (Maynard Smith & Parker 1976; Field & Hardy 2000; Kemp 2000).

Later work has extended the basic games, limiting the conditions under which paradoxical solutions can evolve (Enquist & Leimar 1987; Mesterton-Gibbons 1992; Mesterton-Gibbons & Adams 1998), yet in the majority of conflict games, paradoxical solutions remain a feature (Hammerstein & Parker 1982; Parker 1984; Enquist & Leimar 1987; Field & Hardy 2000). For example, Mesterton-Gibbons (1992) analysed owner-intruder games, and found parameter regions where a common-sense 'bourgeois' (aggressive owners) strategy prevailed. This, however, required an *a priori* assumption that owners are more likely to win fights; otherwise, the paradoxical 'anti-bourgeois' strategy became more likely.

Here, we consider a particular case of paradoxical versus common-sense strategies, one of crucial importance during initial settlement of previously unoccupied space: if winners and losers of fights behave differently, why should the winner, rather than the loser, become more daring in future fights and claim ownership of an area, all else being equal? If the loser became the new owner, the outcome would share features of other paradoxical solutions. Such an outcome appears counterintuitive, yet if the outcome of a fight is a simple asymmetry whose outcome is largely determined by chance, an ESS could equally well dictate one or the other experience (win or lose) to be used as the cue that makes an animal retreat.

Studies have shown that while common-sense solutions (including both owners winning and larger, or higher RHP, individuals winning) are common in many taxa (fish: Beaugrand et al. 1996; Chellappa et al. 1999; birds: Tobias 1997; insects: Petersen & Hardy 1996; Alcock & Bailey 1997; crustaceans: Jennions & Backwell 1996; mammals: Barnard & Brown 1984), paradoxical solutions are (almost) non-existent. Maynard Smith (1982) quotes studies (Burgess 1976) on *Oecibus civitas* spiders as showing potentially paradoxical behaviour. Owners of webs give up their webs to intruders, leading to a pattern of repeated displacements. We are, however, unaware of any follow-ups documenting the same patterns in this or other species (for a current debate concerning butterflies, see Hernandez & Benson 1998; Field & Hardy 2000; Kemp 2000). Furthermore, the above example relates to owner-intruder asymmetry, rather than winner-loser asymmetries which are relevant when occupying new areas.

This points to a surprisingly unresolved question in the first application of game theory to the study of animal behaviour: if theory continues to predict paradoxical solutions under certain conditions, why do we only ever observe common-sense solutions in nature? Our game theory approach to the problem of winning space evaluates the stability of both paradoxical and common-sense solutions.

Methods

THE MODEL: BACKGROUND INFORMATION

Animals compete for access to areas containing necessary resources such as food and nest sites. We can imagine a situation in which two individuals are in conflict over such a space, in an attempt to either extend their current territory or establish a new one. Both individuals are able to withdraw from the contested area to an uncontested area (for example, the core of their existing territory). We aim to investigate the strategies that individuals might use in the course of this pairwise conflict.

A strategy must specify precisely the behaviour of an individual in every possible situation (von Neumann & Morgenstern 1953; Maynard Smith & Parker 1976; Broom et al. 1997). A fight between two contestants can end either in one of them winning, or in a draw, after which each individual will make a decision on how likely it is to return to the location of the fight in the future. This combination of probabilities makes up an individual's strategy. Thus, we define a strategy S = $\{S_W, S_L, S_D\}$, where S_W is the probability of returning to the fight location after winning the fight, S_L is the probability of returning having lost, and S_D is the probability of returning when the fight has ended in a draw. As each probability can take any value from zero to one the strategy set is continuous (Parker 1984), and a potentially infinite number of strategies can be used (see table 4.1 for parameter definitions).

We consider situations in which a mutant individual using a strategy $\mathrm{S_m} = \{S_{mW}, S_{mL}, S_{mD}\}$ is in conflict with a single member of a population using strategy $\mathrm{S_{pop}} = \{S_{pW}, S_{pL}, S_{pD}\}$. We aim to investigate which population strategies are evolutionarily stable against invasion by $\mathrm{S_m}$ by calculating a measure of the mutant individual's fitness when $\mathrm{S_m} = \mathrm{S_{pop}}$ and when $\mathrm{S_m} \quad \mathrm{S_{pop}}$.

In terms of this model, a common-sense strategy would be one such as S = {0.8, 0.2, 0.5}, where the animal returns more frequently when it has won than when it has lost. A paradoxical strategy would be one such as S = {0.2, 0.8, 0.5} where the probability of returning having lost is greater than the probability of returning having won. In investigating the stability of paradoxical strategies, we ask whether a strategy in which the probability of returning after losing exceeds the probability of returning after winning can ever be an ESS.

In order to investigate the effect of different return strategies on the mutant individual's fitness, we need to consider at least two fights between the contestants. For simplicity, we restrict our analysis to a contest involving exactly two fights, the smallest number we can use to investigate how the outcome of one fight affects an individual's behaviour in the next. Throughout, 'fight' refers to a single aggressive interaction between two individuals, while 'contest' refers to a series of fights (in this case, two).

Table 4.1: Model parameters and definitions (see the text for detailed descriptions of each parameter)

Parameter	Definition
$S = \{S_W, S_L, S_D\}$	Strategy used by an individual, composed of the probability that it returns to the contested area in response to winning, losing, and the fight ending in a draw
α	Proportion of the population that is of high RHP
T	Type of fight (competitors equal or differing in fighting ability)
a	Degree of asymmetry between the two classes of individuals in the population
p	Probability of an individual winning a given fight
q	Probability of an individual losing a given fight
p_d	Probability that a fight ends without a winner and loser (a draw)
v	Value (benefit) gained from an unsettled contest
V	Value (benefit) gained from a settled contest
c_W	Cost associated with winning a given fight
c_L	Cost associated with losing a given fight
c_D	Cost associated with participating in a fight which ends in a draw
δ	Amount of error in decision making (behavioural variability)

We consider three potential outcomes to the contest, depending on which of the two competing individuals chooses to return to the contested area. The mutant individual may not return after the second fight, in which case it gains no increase in fitness from the contest (it may suffer losses; see section on 'costs' below). If the mutant individual returns but the opponent does not, we assume that the contest has been settled, and the individual gains a large fitness benefit from becoming the sole occupier of the disputed space. If both individuals return, we assume that no further aggressive interaction takes place and the space is shared between the competitors. In this case, we consider the contest to be unsettled, and a smaller benefit is gained by each contestant from the use of the space.

To investigate the effect of differences in fighting ability on the strategies that individuals use, we assume that the population consists of two classes of individuals, those of good fighting ability or high RHP, and those of lower fighting ability or low RHP. We assume that a fraction α of the population is of high fighting ability (Type 1 individuals; type 0 individuals are those of low fighting ability). In such a population, $T_E = \alpha^2+(1-\alpha)^2$ of fights will occur between equal individuals, in $T_S = \alpha(1-\alpha)$ of cases, the mutant individual will be of high RHP (Type 1), fighting against an individual of poor fighting ability (Type 0), and in $T_W = (1-\alpha)\alpha$ of cases, it will be of low RHP, fighting against a good fighter, assuming spatially random mixing of individuals. Thus, when calculating individual fitness (see below) we take a weighted mean of the fitness for the three types of fight. Throughout this paper, we use $\alpha = 0.5$. Testing other values is beyond the scope of this paper, but would follow the same principles as described here. Individuals are assumed not to know their own fighting ability. They can, however, observe the outcome of the first fight and adjust their behaviour accordingly.

FIGHT OUTCOMES

As described above, fights may end up in wins, losses and draws. When two equally matched competitors meet, it is natural to assume that the probability of winning equals the probability of losing: $p = q$; additionally, p_d describes the probability of a fight ending in a draw. We use subscripts such as '10' to denote a high-RHP individual fighting against a low-RHP individual. Where two high-RHP players (1), or two low-RHP players (0) meet, the probabilities of winning, p_{11} and p_{00}, and the probabilities of losing, q_{11} and q_{00}, are

$$p_{11} = p_{00} = q_{11} = q_{00} = \left(\frac{1-p_d}{2}\right) \tag{1}$$

In fights between and high- and low-RHP players, $p > q$ for the high RHP individual. For simplicity, and to allow us to investigate the impact of varying a single parameter on the ESS, we assume that a fixed proportion of fights end in a draw for each set of parameter values. The limitations of this assumption are discussed later (see Discussion). The probabilities of winning and losing in fights that occur between individuals of differing competitive ability are calculated from the asymmetry in fighting ability between individuals in the population, described by a. This parameter can take values from zero to one. If a takes a value of 1, then in fights between unequal competitors where there is a winner, the victor will always be the individual that is of higher RHP. In asymmetrical situations, the probability that an individual with good fighting ability wins against a poor fighter, p_{10}, and therefore that a poor fighter loses to high RHP individual, q_{01}, is

$$p_{10} = q_{01} = \left(\frac{1+a}{2}\right)(1 - p_d) \tag{2}$$

Likewise, the probability that individual with high RHP loses to a poor player, q_{10}, and the probability that an individual with low RHP wins over a good player p_{01}, is

$$p_{01} = q_{10} = \left(\frac{1-a}{2}\right)(1 - p_d) \tag{3}$$

In the special case where a takes a value of zero, all individuals in the population are identical in fighting ability. Note that when $a = 0$, the types 1 and 0 become identical, and the model produces identical results regardless of the value of α. For the sake of simplicity we have kept $\alpha = 0.5$ for these cases too. At any other value of a the individuals belonging to different groups have true differences in fighting abilities, even though these differences may be slight.

We use the outcome probabilities above, S_m, and S_{pop} to calculate the probability of each contest outcome (series of two fight outcomes; table 4.2). In T_E fights, where individuals are equal, we use p_{11}, p_{00}, q_{11} and q_{00}. In T_S fights, where the mutant is stronger, we use p_{10} and q_{10}, and in T_W fights; where the mutant is weaker, we use p_{01} and q_{01}.

Table 4.2: Calculation of probabilities associated with each outcome, from the point of view of the mutant individual.

First fight	Second fight				
	win	lose	draw	no opponent	avoid
win	$P_{ww} = pS_{mW}S_{pL}\,p$	$P_{wl} = pS_{mW}\,S_{pL}\,q$	$P_{wd} = pS_{mW}S_{pL}p_d$	$P_{we} = pS_{mW}\,(1\text{-}S_{pL})$	$P_{wa} = p(1\text{-}S_{mW})$
lose	$P_{lw} = qS_{mL}\,S_{pW}p$	$P_{ll} = qS_{mL}\,S_{pW}q$	$P_{ld} = qS_{mL}\,S_{pW}p_d$	$P_{le} = qS_{mL}\,(1\text{-}S_{pW})$	$P_{la} = q(1\text{-}S_{mL})$
draw	$P_{dw} = p_d\,S_{mD}\,S_{pD}p$	$P_{dl} = p_dS_{mD}\,S_{pD}\,q$	$P_{dd} = p_dS_{mD}\,S_{pD}p_d$	$P_{de} = p_dS_{mD}\,(1\text{-}S_{pD})$	$P_{da} = p_d(1\text{-}S_{mD})$

COSTS OF FIGHTING

The costs associated with fighting are described by c_W (cost of winning a fight), c_L (cost of losing a fight) and c_D (cost of participating in a fight that ends in a draw). To remain biologically meaningful, we assume that the cost of losing a fight must always exceed the cost of winning. We will consider the limitations of this assumption in the Discussion. As studies have shown that the costs of aggression are positively related to the duration or intensity of aggressive encounters (e.g. Hack 1997; Neat et al. 1998a), we assume that all encounters ending with a specific outcome (win, loss or draw) are equal in duration and/or intensity, and so are equally costly. Where competitors are unequal, we assume that the costs of a specific outcome are the same whether the individual is of good or poor fighting ability. We do not currently include an asymmetry in the ability to bear the costs of an aggressive encounter.

Contest costs are calculated from the cost of a fight outcome, c_W, c_L or c_D, multiplied by the probability of that outcome in the first and second fights; we assume that the cost of successive fights are independent of each other. The likelihood that an individual wins one of the two fights in which it is involved (P_{W1}) is the sum of the probabilities of winning the first fight, when the outcome of the second fight was a loss or a draw, or one or both of the competitors did not return for the second, plus the sum of the probabilities of winning the second fight, when the first fight ended with a loss or draw for the individual in question (table 4.2). Thus:

$$P_{W1} = P_{wl} + P_{wd} + P_{we} + P_{wa} + P_{lw} + P_{dw} \tag{4}$$

The subscripts w, l, d, refer to an outcome of a win, loss or draw in the first (first position) or second (second position) fight. In the case where the opponent does not return, we use the subscript e, and where the mutant does not return, a. The probability of winning both fights is described by P_{ww}. The probabilities of losing and drawing in one and both fights are calculated analogously to equation (4) and P_{ww}. The total costs associated with fighting are:

$$C = c_W(2P_{ww} + P_{W1}) + c_L(2P_{ll} + P_{L1}) + c_D(2P_{dd} + P_{D1}) \tag{5}$$

BENEFITS OF FIGHTING

The benefits gained from ownership of the disputed territory are described by v and V for unsettled and settled contests, respectively. In an unsettled contest, both contestants return after the second fight. In this case, the mutant has access to a resource of value v. In a settled dispute, where the opponent does not return after the first or second fights and the mutant has sole use of the disputed territory, the resource has a value of V. V is always equal to or greater than v. The actual benefits gained from settled contests, B_S, are calculated from the probability of the contest being settled (the sum of table 4.3a) multiplied by V. Benefits from unsettled contests, B_U, are calculated from the probability of contests where both the mutant and the opponent return after the second fight (the sum of table 4.3b), multiplied by v. No benefits are gained when the mutant does not return after the first or second fight.

Table 4.3: Return probabilities after the second fight. Only the mutant returns (a) and both competitors return (b)

a)

First fight	Second fight				
	win	loss	draw	no opponent	avoid
win	$M_{ww}=P_{ww}S_{mW}(1-S_{pL})$	$M_{wl}=P_{wl}S_{mL}(1-S_{pW})$	$M_{wd}=P_{wd}S_{mD}(1-S_{pD})$	$M_{we}=P_{we}$	0
loss	$M_{lw}=P_{lw}S_{mW}(1-S_{pL})$	$M_{ll}=P_{ll}S_{mL}(1-S_{pW})$	$M_{ld}=P_{ld}S_{mD}(1-S_{pD})$	$M_{le}=P_{le}$	0
draw	$M_{dw}=P_{dw}S_{mW}(1-S_{pL})$	$M_{dl}=P_{dl}S_{mL}(1-S_{pW})$	$M_{dd}=P_{dd}S_{mD}(1-S_{pD})$	$M_{de}=P_{de}$	0

b)

First fight	Second fight				
	win	loss	draw	no opponent	avoid
win	$R_{ww}=P_{ww}S_{mW}S_{pL}$	$R_{wl}=P_{wl}S_{mL}S_{pW}$	$R_{wd}=P_{wd}S_{mD}S_{pD}$	0	0
loss	$R_{lw}=P_{lw}S_{mW}S_{pL}$	$R_{ll}=P_{ll}S_{mL}S_{pW}$	$R_{ld}=P_{ld}S_{mD}S_{pD}$	0	0
draw	$R_{dw}=P_{dw}S_{mW}S_{pL}$	$R_{dw}=P_{dl}S_{mL}S_{pW}$	$R_{dd}=P_{dd}S_{mD}S_{pD}$	0	0

CALCULATING FITNESS

Fitness is defined as the difference between the benefits of using the space and the costs paid during the contest. For example, we can imagine a situation where the population is using strategy $S_{pop} = \{0.5, 0.5, 0.5\}$, and a mutant individual uses strategy $S_m = \{0.1, 0.2, 0.8\}$. To present a simple example, we assume that in this case no fights end in a draw ($p_d = 0$) and all individuals are equal with respect to their fighting ability ($a = 0$). Other parameters are set as $v = 1$, $V = 5$, $c_W = 0.1$, $c_L = 0.2$ and $c_D = 0.1$. We calculate the costs paid by the mutant when fighting members of the population as C = 0.1613. Unsettled gains $B_U = 0.0056$ and settled gains $B_S = 0.4031$. Fitness of the mutant, W, is calculated as:

$$W = B_U + B_S - C \tag{6}$$

and thus is equal to 0.2474.

FINDING THE ESS

To find the strategies that are evolutionarily stable, we check whether the population strategy can be invaded by a mutant using a different strategy, then we check if it can be invaded by another mutant strategy, until all possible mutants have been checked. An evolutionary stable strategy occurs when all mutants deviating from the population strategy have lower fitness than the population strategy, meaning that the population strategy can not be invaded by an alternative strategy.

Returning to the previous example, we can calculate whether or not the mutant strategy S_m is able to invade a population that is using strategy S_{pop}. We calculate the fitness of a random member of the population (i.e. an individual using S_{pop}) against the population as a whole. In this case, W for S_{pop} equals 0.375. Comparing this to the fitness of the mutant using S_m against S_{pop} (0.2474), we see that the population member has higher fitness than the mutant, and thus the population is stable against invasions by a mutant using S_m.

As there are a potentially infinite number of strategies that can be tested, it is impossible to test them all in the manner outlined above. Instead, we use convergence techniques (Houston & McNamara 1999) to find ESSs. A standard technique for finding an ESS in a dynamic game is through iteration of the best response map (McNamara et al. 2000). This procedure starts with an arbitrary strategy and finds the sequence of strategies where each strategy is the best response to the previous strategy in the sequence. A problem of this method is that the sequence sometimes oscillates without converging towards the ESS. By incorporating errors in decision making, oscillation can be eliminated. 'Errors' here refer to the biologically realistic assumption that individuals do not always use the strategy that yields them highest fitness, especially if the fitness difference between two options (e.g. return or do not return to an area) is small. By including errors, it is thus assumed that the probability of making an error decreases as the cost of making it increases (McNamara et al. 1997).

As a strategy S consists of S_W, S_L and S_D, we vary each in turn to find the best response, and update S. We calculate fitness for an animal using (in the first instance) $S_W = 1$ or $S_W = 0$, against a member of the population using S_{pop}. Denoting the fitness of the strategy $\{1, S_L, S_D\}$ by W_1 and that of $\{0, S_L, S_D\}$ by W_0, we can calculate the fitness difference between using $S_W = 1$ and $S_W = 0$ as $d = W_1 - W_0$. The best response with error (behavioural variability) is then calculated as

$$S_{Wn} = \left(\frac{1}{1 + e^{-d/\delta}} \right) \tag{7}$$

The amount of error is indicated by the parameter δ. Increasing δ means more variability in behaviour: if δ is small, the animal is highly likely to choose the better option even if the fitness difference between the two behavioural options is small. As δ approaches infinity, the individual chooses either action with a probability that approaches 1/2: animals become increasingly unable to differentiate between actions with similar consequences. Using this method, the value for S_{Wn} depends on the fitness consequences of the two options ($S_W = 1$ and $S_W = 0$) when they compete against a population using S_{Wn-1}. Other components of the strategy (S_L and S_D) are calculated analogously.

The iteration then proceeds as follows:

1. Choose an initial population strategy $S_0 = \{S_{W0}, S_{L0}, S_{D0}\}$.

2. Calculate S_{W1} according to equation (7).

3. Calculate S_{L1} analogously to equation (7).

4. Calculate S_{D1} analogously to equation (7).

5. Create the new $S_1 = \{S_{W1}, S_{L1}, S_{D1}\}$.

6. Repeat steps 2 to 5 to find the new population strategy S_2.

Steps 2 to 6 are repeated over n time-steps. This quickly produces an ESS where $S_n = \{S_{Wn}, S_{Ln}, S_{Dn}\}$.

Results

By altering the values given to the various parameters, we investigated the ESS solutions that emerged from the model under different conditions.

IS AVOIDANCE BEHAVIOUR ADAPTIVE?

First, we investigated whether it is adaptive for both winners and losers (or for individuals who experienced a draw) to avoid areas of conflict. We found no situations in which both previous winners and losers avoided the contested area completely. However, figure 4.1 shows that in some cases (low value of V), individuals return with less than 50% probability no matter what the outcome of the previous fight. This confirms that avoidance behaviour is indeed sometimes beneficial regardless of the outcome of the fight; also note that a return probability of less than 50% guarantees that the result is not merely due to errors in decision-making (random variation in behaviour), but that staying away truly generates higher fitness than returning. This is intuitive: when the benefits (V) are small compared to the costs of meeting an opponent and fighting. Likewise, there is an intuitive explanation as to why complete avoidance behaviour (neither competitor ever returns to the area of conflict) nevertheless does not evolve: if one participant (say, the loser) always stays away, there is no cost for the other (say, the winner) to return and claim the reward V.

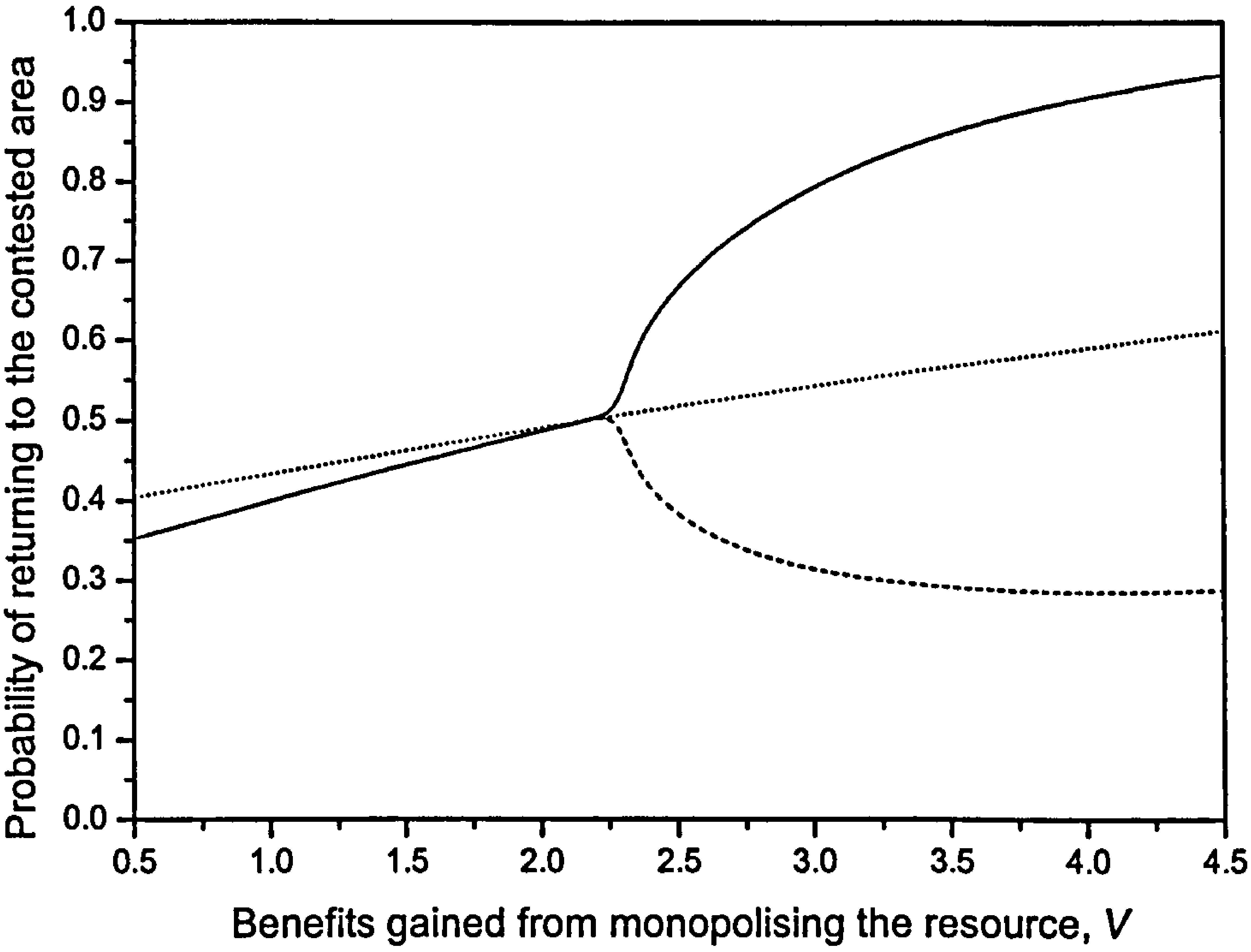


Figure 4.1: Evolutionarily stable return probabilities after winning (S_W, solid line), losing (S_L; dashed line) and after a draw (S_D; dotted line), for a population starting its evolution from a common-sense strategy $S_{pop} = \{1, 0, 0.5\}$. Other parameter values used: $\alpha = 0.5$, $v = 1$, $c_W = 2.5$, $c_L = 5$, $c_D = 2.5$, $a = 0$, $p_d = 0.2$, $\delta = 0.5$; value of resource V as indicated on the x axis. In some cases (when the value of monopolising the resource, V, is low), both winners and losers avoid the contested area more than half the time, at other times, winners return but losers avoid the area (high V).

COMMON-SENSE VS. PARADOXICAL SOLUTIONS

We define a paradoxical solution as one where the probability of returning having won a fight is lower than the probability of returning having lost. In figure 4.1, all solutions were derived assuming that $S_{pop} = \{1, 0, 0.5\}$ was the ancestral strategy from which evolution starts. This strategy is common-sense, and it is therefore not surprising that solutions are common-sense too (figure 4.1). We now turn to the question of whether common-sense and paradoxical solutions are equivalent in the model. In other words, if evolution starts from a common-sense or a paradoxical strategy (the initial population strategy), will stable solutions turn out common-sense or paradoxical?

If solutions are entirely based on conventions, then the convention 'losers return, winners do not' is as logical as the one that specifies the opposite. However, if true fighting ability plays a role, we might expect that winners of the first fight (who are more likely to be good than bad fighters) are more likely to win the latter fight too. Therefore, they suffer lower fighting costs, and should be more prone to return than losers. This would lead to the evolution of a common-sense strategy even if starting from a paradoxical ancient strategy.

Figure 4.2 shows how δ (the magnitude of behavioural variability) and a (the asymmetry between individuals) affect whether both paradoxical and common-sense strategies can be stable, or whether a common-sense strategy evolves irrespective of whether the ancient population was common-sense or paradoxical. When animals adhere to a behavioural rule without much variation (small δ), both types of population strategies are stable regardless of the asymmetry between individuals.

When behaviour is more variable (large δ), asymmetries between fighters allow common-sense solutions to evolve from paradoxical population strategies. Thus, when the difference between good and poor fighters is large, paradoxical strategies are unlikely to be stable, except when behaviour shows little random variation.

Figure 4.2 also shows how the stability of paradoxical strategies is affected by the relative costs and benefits of fighting. Figure 4.2a shows that when both costs and benefits are high, paradoxical solutions persist over much of the parameter space, evolving to common sense solutions only when variability δ and asymmetries in fighting ability a are high. When the costs of fighting are reduced (figure 4.2b), common sense solutions evolve from paradoxical ancestral strategies when there is less variation in behaviour (lower δ) and asymmetries are smaller (lower a). A similar pattern is seen when the benefits of fighting are reduced (figure 4.2c). Finally, figure 4.2d shows that when both the costs and benefits of fighting are low, common sense solutions prevail over the majority of the parameter space. Paradoxical solutions are only stable when there is very little behavioural variation (small d) and animals differ only slightly in their fighting ability (small a). Additionally, paradoxical solutions are stable when all individuals are identical with respect to their fighting ability ($a = 0$).

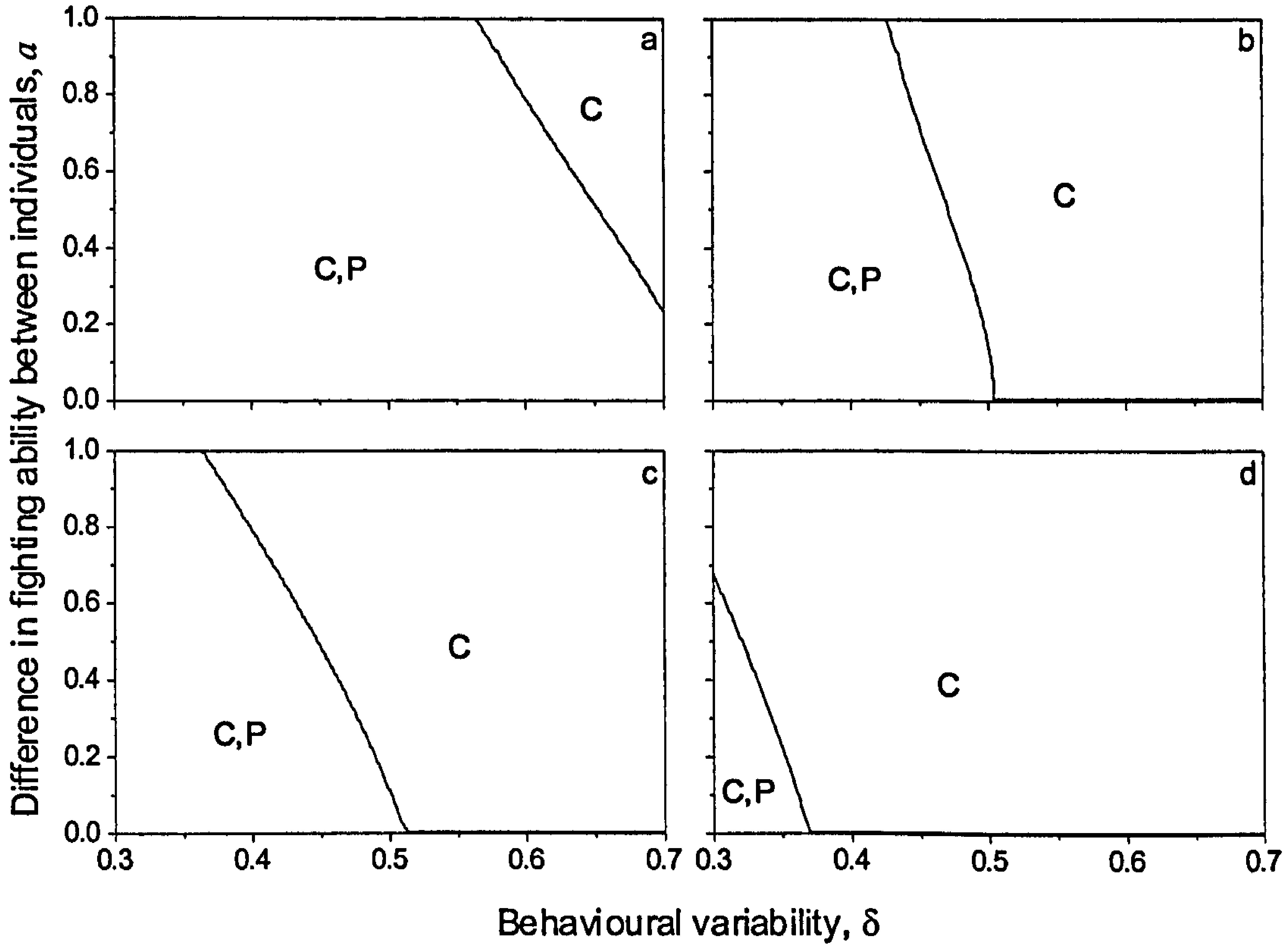


Figure 4.2: Stability of common sense (C) and paradoxical (P) strategies at various values of behavioural variability (δ) and population-wide difference in fighting ability (*a*). Where both C and P exist, either can be stable depending on the initial strategy in the ancient population. Each panel shows stabilities for different values of monopolising the resource, *V*, and costs of fighting c_W, c_L and c_D. (a), $V = 5$, $c_W = 3$, $c_L = 6$, $c_D = 3$ (b), $V = 5$, $c_W = 2$, $c_L = 4$, $c_D = 2$ (c), $V = 2$ $c_W = 3$, $c_L = 6$, $c_D = 3$ and (d) $V = 2$, $c_W = 2$, $c_L = 4$, $c_D = 2$. Other parameter values used for all panels: $\alpha = 0.5$, $v = 1$, $p_d = 0.2$. Ancient strategies: for common sense, $S_{pop} = \{1, 0, 0.5\}$; for paradoxical, $S_{pop} = \{0, 1, 0.5\}$.

STRENGTH OF CONVENTIONS

A convention is a rule based on arbitrary cues that allows quick resolution of potentially protracted disputes (Mesterton-Gibbons & Adams 2003). In game theory, 'convention' is generally used to describe pure strategies (Maynard Smith & Parker 1976; Parker 1984), however, we use a slightly broader meaning: we assume that behaviour can vary (McNamara et al. 1997), and thus we do not obtain pure strategies. We have therefore used 'convention' to mean a situation where either one of two possible outcomes (winning, losing) can equally well function as the cue that makes an animal to return to the contested area, and it is sufficient that the behaviour is statistically associated with the cue.

When a paradoxical solution is stable, it means that animals rely on a convention to settle fights: one outcome (losing) determines a higher probability of returning, which could lead to ownership even though it does not have a positive relationship to the ability to defend a territory. We have demonstrated that conventional behaviour of this type can be stable if fighting ability does not differ much between individuals, and they follow behavioural rules strictly (figure 4.2).

Figure 4.3a shows the common-sense solution in a case where individuals do not differ in fighting ability at all ($a = 0$). Thus, their fate in the first fight does not give them any information about their fighting ability; if they nevertheless adjust their behaviour according to the fight outcome, it must be due to a convention. The asymmetry in fight outcome is the only factor influencing the choice of strategy, equivalent to role asymmetries (such as owner or intruder) determining outcomes in other game theory models (Maynard Smith & Parker 1976; Maynard Smith 1982;

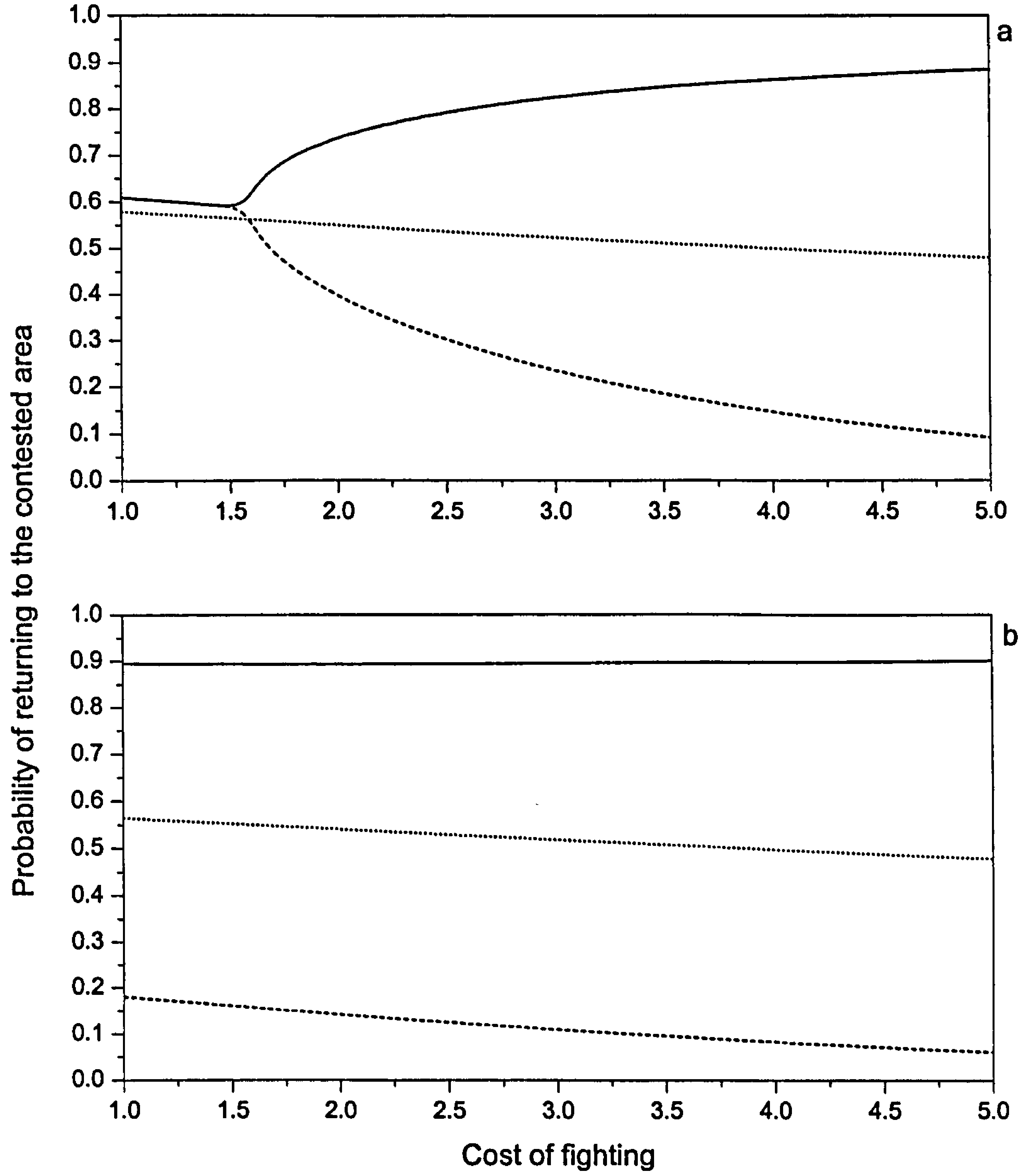


Figure 4.3: Return probabilities with (a) $a = 0$, (b) $a = 1$. Solid line: ESS probability of returning having won, dashed line: probability of returning having lost, dotted line: probability of returning after a draw. Parameter values used: $\alpha = 0.5$, $c_L = 6$, $v = 1$, $V = 3$, $p_d = 0.2$, $\delta = 0.5$, initial $S_{pop} = \{1, 0, 0.5\}$. Cost of winning (c_W) and a draw (c_D) as indicated on the x axis.

Leimar & Enquist 1984; Enquist & Leimar 1987). Conventions clearly become stronger when the costs of fighting increase: winner and loser behaviour becomes markedly different when fighting costs are large (figure 4.3a). In the case where there are true differences in fighting ability (figure 4.3b), losers gain information about their fighting ability in the first fight, and they consequently avoid the area even if costs of fighting are low.

Additionally, as the value of sharing the resource, v, increases, the probability of losers returning increases (not shown). This is intuitive; when a resource is worth sharing (high v), it makes sense for both winners and losers to return to claim a part of it, even though this may involve further aggressive interactions.

Discussion

IS AVOIDANCE ADAPTIVE?

Contrary to the assumptions of some models (Stamps & Krishnan 1999, 2001), our results suggest that a tendency to avoid areas in which fights have occurred is not always an adaptive strategy for territorial animals. In some cases, however, avoidance behaviour is beneficial, no matter what the outcome of the fight (low values of V, figure 4.1). This is intuitive when the benefits (V) of fighting are small compared to the costs of meeting an opponent and fighting.

An interesting phenomenon is that the probability of returning can decrease with increasing value (V) of the resource. This happens for losers of fights when winners become much more prone to return after fights, which in turn increases the costs of returning to losers (figure 4.1). At large values of V, individuals respond to winning by returning to the area. When losers do not do so, winners have effectively claimed ownership of the area (figure 4.1, large V). When one participant (in this case, the loser) stays away, it makes sense for the other (the winner) to return to the contested area and claim the benefits V. As it is unlikely to meet the loser again, there are no costs associated with returning.

In their model of territory acquisition by unequal competitors, Stamps and Krishnan (2001) found that individuals suffering lower fighting costs acquire larger territories than individuals suffering from higher fighting costs. In the current model, when the benefits are higher, winners (who suffer lower fight costs) have a higher tendency to return to the contested area than losers, which could lead to the establishment of larger territories. Our model thus also supports the finding that the costs experienced by an individual could affect their final territory size (Stamps & Krishnan 2001).

Additionally, our findings support the assumption of early game theory models that animals can win space by winning fights (Maynard Smith & Price 1973; Grafen 1979; Maynard Smith 1982), if their opponent avoids the area having lost. The costs of fighting relative to the benefits of winning determine whether general avoidance (as in Stamps & Krishnan 1999, 2001) or a 'winner-takes-all' pattern evolves.

COMMON-SENSE VS. PARADOXICAL SOLUTIONS

We also found that sometimes paradoxical (losers have a higher probability of returning than winners) and common-sense (winners are more likely to return) solutions both exist and at other times, only common-sense strategies are stable (figure 4.2). This reflects the findings of other game theory models, which show a limited set of conditions under which paradoxical strategies can evolve (Maynard Smith & Parker 1976; Hammerstein & Parker 1982; Enquist & Leimar 1987; Mesterton-Gibbons 1992). Variation in fighting ability, a, variability in behaviour, δ, and the costs and benefits of fighting play a role in determining whether a paradoxical ancestral population strategy evolves to a common-sense or paradoxical solution in the current game. Why is this the case? When individuals differ little in fighting ability (small a), an individual gains little information on its own RHP from fighting. Overly high fight costs can then be avoided simply based on conventions, and paradoxical strategies can remain stable. When there are large differences in fighting ability (large a), winners of the first fight (likely to be of high RHP) are likely to also win the second fight, suffer lower fighting costs and be more likely to return than losers. This leads to the evolution of a common-sense strategy even when the ancestral strategy is paradoxical.

However, even when differences in fighting ability exist, paradoxical strategies can be stable if animals adhere strictly to behavioural rules (small δ). This means that an initial convention that was in use in an ancient population remains stable. But when there is some behavioural variability (large δ), individuals who in reality are better fighters sometimes return to contested areas even if the initial convention dictates they should not. As these individuals tend to win, the convention is broken down, and true fighting ability takes over as a decisive feature of the system.

When the costs and benefits of fighting are low, paradoxical solutions are no longer stable, and evolve to common sense ESSs (figure 4.2). When the benefits are low, losers can no longer offset the high costs of losing by returning to claim the resource, and so gain higher fitness by not returning, and the paradoxical convention is broken down. Conventions also tend to break down when benefits of fighting are low. This implies that the fitness difference between returning and avoiding is small. The cost of making errors is thus small, and therefore errors occur more frequently (McNamara et al. 1997), which in turn implies that selection does not strongly prevent individuals from choosing the alternative behaviour. When original rules of behaviour are not strictly followed, the signature of the true fighting ability can become dominant, and a common-sense ESS evolves.

Our finding that fighting ability plays a greater role in settling disputes when the asymmetry in fighting ability is greater is not surprising. Many empirical studies show that body size (generally an indicator of fighting ability) plays an important role in determining the outcome of fights (Jennions & Backwell 1996; Beaugrand et al. 1996; Petersen & Hardy 1996; Johnsson et al. 1999). The finding that conventions can be important when asymmetries are small is reflected in empirical studies where owners tend to win fights against intruders when their fighting ability appears to be equal to or lower than that of their opponent (Beaugrand et al. 1996; Jennions & Backwell 1996; Alcock & Bailey 1997; Chellappa et al. 1999; Johnsson et al. 1999; Wenseleers et al. 2002).

However, it has been suggested that residents tend to win not because of arbitrary conventions but because they have greater motivation to fight, as their valuation of the resource is greater, a finding supported by empirical data (birds, Krebs 1982; Tobias 1997; fish, Neat et al. 1998b; Johnsson & Forser 2002; insects, Alcock & Bailey 1997; crustaceans, Edsman & Jonsson 1996). Our results suggest that conventions are not necessarily falsified if some asymmetry (e.g. in resource-holding potential, or in valuing the resource) can be shown to exist. While avoidance behaviour by the loser is stronger when asymmetries exist (figure 4.3b), it persists in the absence of asymmetries too (figure 4.3a).

As the costs of fighting increase, strategies where winners return with increasing probability and losers with decreasing probability become stable (figure 4.3). This suggests that as fighting becomes costly, conventions become stronger even if strategies are common-sense (note that the information content gained by the initial fight does not change when costs change). If fighting is costly, then it would benefit individuals to avoid fighting whenever possible, and a strategy where only one of the contestants would return would allow animals to avoid a second fight in that location but enable one of them to gain the benefits associated with returning to it. As the benefit associated with monopolising the resource, V, increases (figure 4.1), we also see an increasing difference in the behaviour of winners and losers. As paradoxical strategies are stable at high values of V (figure 4.2), this suggests that conventions play a role here, too, otherwise we would expect the individual of greater fighting ability to always return more frequently and a common-sense solution to emerge.

According to our results, the fact that paradoxical strategies are not seen in nature probably relates to the fact that fighting abilities indeed almost always vary between individuals, and there usually is some behavioural variation (as in almost any biological trait). This highlights the general importance of not assuming that individuals always optimise their behaviour in every single instance (McNamara et al. 1997). In addition, paradoxical strategies are not seen when the costs and benefits of fighting are low. In nature, animals probably do not engage in extremely costly fights for small areas of extremely valuable space. Instead, low cost aggression, such as chases and displays, rather than escalated fights, is common (butterflies, Davies 1978; Hardy 1998; damselflies, Waage 1988; spiders, Riechert 1978; lizards, Stamps & Krishnan 1997, 1998). Additionally, the patches of space contested may be relatively low in value in comparison to an entire territory, for example, when individuals are contesting small areas of feeding territories rather than the centre of a breeding territory.

LIMITATIONS OF THE MODEL

As with all models, we have made some assumptions that should be evaluated critically. Individuals in our model only gain information regarding their fighting ability from the fights; they do not know their own fighting ability beforehand. A longer series of fights would enable an individual to gain more accurate information, as each fight would enable them to update the information they possess (Enquist & Leimar 1983). If individuals can gain more accurate information, or have prior information regarding their fighting ability, common-sense solutions would be strengthened as individuals would be able to more accurately assess their chances of winning or losing a fight and participate or avoid accordingly.

In addition, the 'winner and loser' effect (Dugatkin 1997; Hsu & Wolf 1999; 2001) may have an influence on the behaviour of an individual. According to this effect, an animal is more likely to win (lose) in fights following a fight that it has already won (lost). In our model, winning probabilities themselves do not change as a result of prior experience. However, the fact that winners become more daring in terms of returning to the area could be interpreted as similar to the winner effect. Winner effects clearly have the potential to further enhance the stability of common-sense solutions.

In the model, we assume that the parameters describing asymmetries in fighting ability, a, and the probability that fights end in a draw (p_d) are independent. Although one could expect that draws would occur more frequently when individuals are equally matched (possibly with draws occurring 100% of the time), there are also situations in which equally matched competitors fight until there is a clear winner (Davies 1978; Waage 1988; Gribbin & Thompson 1991; Kemp & Wicklund 2001), and likewise, there are situations where draws occur even though one would expect the better fighter to win (Stamps & Krishnan 1997). It is important to note that the model is able to produce solutions for any given combination of fight outcome probabilities that may occur in nature.

We assume a relationship between the outcome of a fight and its cost, namely that losing is always more costly than winning. A limitation of this assumption is that this relationship between fight outcome and associated cost does not hold true for all species. Experimental studies have shown that while in some cases, losers do incur higher costs than winners (Chellappa & Huntingford 1989; Neat et al. 1998a), in other cases there is no difference in the costs incurred (Smith & Taylor 1992). The energetic cost spent by winners may even exceed that of losers (Hack 1997), which presumably could lead to a wider diversity of outcomes than we have derived. For simplicity, we also assume that all fights ending in the same outcome carry the same cost. This can be viewed as an average cost, as an aggressive interaction can take many different forms, ranging from threat display and avoidance to escalated contests, which are likely to carry very different costs to both the winner and the loser (Chellappa & Huntingford 1989; Smith & Taylor 1992; Brick 1998; Neat et al. 1998a).

Experimental findings suggest that territory owners abandon territory defence when the costs of fighting become too high (Carpenter 1987; Tricas 1989). Fighting costs in the experimental studies are generally associated with the number of intruders on the territory (e.g. Myers et al. 1979; Carpenter et al. 1983; Carpenter 1987; Tricas 1989; Keeley 2000; review in Adams 2001). Our model considers the cost of each interaction, rather than the number of interactions, so that there is scope for further study. Considering the dynamics of space use when there are multiple intruders and continuous space, while evaluating the adaptive value of strategies, would be a clear next step in combining the spatially explicit approach of mechanistic models (Stamps & Krishnan 1999; 2001) with the evolutionary aspects of game theory models (see **chapter 5**).

CHAPTER 5

BRIDGING THE GAP BETWEEN MECHANISTIC AND ADAPTIVE EXPLANATIONS OF TERRITORY FORMATION

Abstract

How animals divide space can have fundamental implications for the population dynamics of territorial species. It has recently been proposed that space can be divided if animals tend to avoid fight locations, rather than the winner of fights gaining access to exclusive resources, behaviour that generates exclusive territories in two-dimensional space. A game theory model has shown that this avoidance behaviour can be adaptive, but the adaptiveness has not been investigated in a spatially realistic context. We present a model that investigates potential strategies for the acquisition of territories when two-dimensional space must be divided between individuals. We examine whether exclusive territories form when animals avoid all encounters with others, or only those encounters that have led to losing fights, under different fighting costs and population densities. Our model suggests that when fighting costs are high, and the population density is low, the most adaptive behaviour is to avoid fight locations, which generates well-defined, exclusive territories in a population that is able to resist invasion by more aggressive strategies. Low fighting costs and high population densities lead to the break-down of territoriality and the formation of large, overlapping home ranges. We also provide a novel reason as to why so-called paradoxical strategies do not exist in nature: if we define a paradoxical strategy as an exact mirror-image of a common-sense one, it must respond in the opposite way to a draw as well as to wins and losses. When this is the case, and draws are common (fight outcomes are often not clear-cut in nature), the common-sense strategy is more often adaptive than a paradoxical alternative.

Introduction

Territory ownership is a major determinant of fitness in territorial animals, and the question of how individuals gain territories and partition space can have important implications for the dynamics of populations (Gordon 1997; Both & Visser 2003): exclusive use of space will obviously limit the number of individuals capable of breeding, leading to density dependent effects (e.g. Newton 1992; Rodenhouse et al. 1997; Kokko & Sutherland 1998).

A large body of work considers optimum sizes for territories in an economic framework. These models assume that the costs (in terms of numbers of intruders) and benefits (food resources available) determine territory size, and make predictions concerning the optimal size (e.g. Ebersole 1980; Hixon 1980; Schoener 1983; Schoener 1987). These qualitative predictions have been tested in a range of taxa (Adams 2001). However, the majority of economic models assume that animals are free to adjust their boundaries without constraint from neighbouring territories (Hixon 1980; Schoener 1983; Lima 1984; Adams 2001). In reality, contiguous territories may be compressed below their optimal size by pressure exerted by neighbours (Maynard Smith 1974; Hixon 1980; Patterson 1985; Adams 1998; Keeley 2000; Adams 2001). Clearly, to understand territory formation, it is crucially important to understand the process by which neighbours influence the location of the boundary between territories. Two major lines of thought have emerged: mechanistic models, and models based on adaptive arguments.

Mechanistic models demonstrate the effect of particular rules of behaviour (Adams 2001). Early models used geometric techniques to predict where boundaries are positioned, and suggest that neighbours apply pressure against each other and boundaries are formed where the pressure is equal (e.g. Maynard Smith 1974; Buckley & Buckley 1977; Patterson 1985; Adams 1998; for a review, see Adams 2001). More recent mechanistic models of territoriality are based on animal movement and interactions between neighbours or neighbouring groups of animals. Examples include models of movement and scent marking to predict spatial patterns in timber wolves (*Canis lupus*; Lewis & Murray 1993; White et al. 1996), and the formation of territories as a learning process governed by positive and negative experiences in different locations (Stamps & Krishnan 1999, 2001). Based on observations of territorial settlement in juvenile *Anolis aeneus* lizards, Stamps and Krishnan (1999, 2001) offer a hypothesis where repeated interactions lead to the division of space through 'nagging' (Sih & Mateo 2001). They model a situation in which the attractiveness of an area to an individual depends on the experiences the individual has within it, and individuals only return to areas in which positive experiences (increased familiarity with the area) outweigh negative ones (fights), thus showing a tendency to avoid locations where they have been involved in fights. These models reproduce several features of territorial systems and have much biological realism (Sih & Mateo 2001), but they are mechanistic rather than adaptationist, and do not analyse the costs and benefits of different strategies.

To fully evaluate the underlying assumption of these models that avoidance leads to exclusive space use (Adams 2001; Sih & Mateo 2001), certain factors should be considered. Firstly, models need to be spatially explicit in two dimensions. Additionally, the behaviour of other individuals in the population, and their space use needs to be considered, and for this, game theory modelling is needed. In particular, models should not only consider the behaviour of neighbours, but also their space use and its effects on the availability of space. Few models exist that fulfil all these criteria. Game theory models of territory size (e.g. Parker & Knowlton 1980) tend to be spatially implicit – territories are assumed to spatially contiguous, but the models do not specify the strategies adopted by different neighbours (Adams 2001).

Spatially explicit game theory approaches to the division of space generally consider how two individuals can negotiate the division of a line into two territories (Maynard Smith 1982, Lewis & Moorcroft 2001; Mesterton-Gibbons & Adams 2003; Pereira et al. 2003, Morrell & Kokko 2003; **chapter 4**). As an example of models that use adaptive arguments to explain territory size in two-dimensional space, Both and Visser (2003) modelled the circumstances under which contiguous and non-contiguous territories centred on a nest site should be formed. However, their model fails to satisfy the criterion that individuals' behaviour should influence the availability of space to others: an individual was assumed to be able to expand its territory to a specific size (*T*) regardless of population density, although doing this was costlier at higher densities.

Thus, no model to date satisfies all our criteria. Perhaps closest to achieving this goal, Adler and Gordon (2003) developed a spatially explicit model of territory size in harvester ants, solving for optimal foraging distances. However, the model by Adler and Gordon (2003) is too specific to serve as a general model of space use as it is strongly focussed on the behaviour of ant workers that forage for their colonies.

Here, we develop a model that addresses the issues of multiple competitors and continuous, two-dimensional space, while investigating the adaptiveness of different strategies for territory acquisition. Thus, one of our aims is to combine the spatially explicit approach of mechanistic models with some of the evolutionary aspects of game-theory models, in order to understand the process by which boundaries can form between neighbouring territories.

Model

BACKGROUND

We consider a situation in which a number of individuals, *N*, arrive in a previously unoccupied area of habitat that can potentially be divided into territories. The aim of the model is to determine how the individuals can partition the habitat into separate territories (Stamps & Krishnan 1999, 2001), rather than investigate the decision to contest an existing territory or settle in an unoccupied one (e.g. Mesterton-Gibbons 1992; Broom et al. 1997). Modelling was performed using MATLAB, and an outline of the model code can be found in the Appendix. The habitat area consists of a number of lattice squares, totalling a^2 squares, where a is the linear size of one dimension (i.e. the total number of squares along one edge) of the two-dimensional area. We assume that all squares in the habitat area are of the same intrinsic quality, that is, we assume that every square has the same potential effect on individual fitness. The space used by an individual will consist of more than one of the squares, and the total habitat area is large enough to support the territories of multiple individuals. To avoid boundary effects, the area is wrapped such that each square has exactly four neighbouring squares, and we assume that individuals moving over a boundary arrive back into the habitat area from the opposite side. This is a standard assumption in spatially explicit individual-based modelling (e.g. Slatkin & Anderson 1984; Bascompte & Solé 1997; Ruckstuhl & Kokko 2002).

TERRITORY EXPANSION AND MOVEMENT

We assume that the initial spatial distribution of individuals is random. Each individual therefore begins at a specific ('arrival') location, (i, j), allocated at random, and chosen from all the lattice squares (i.e. 1 i a, 1 j a). Individual k's use of space in square (i, j) at time t is denoted by $A(i, j, k, t)$. This quantity reflects the individual's occupancy of the area, and takes values between 0 and 1. Although 'occupancy' could be taken to imply ownership or exclusive use, we simply mean that this parameter reflects an accumulation of an individual's responses to experiences in the area. An individual uses a square if $A(i, j, k, t) > 0$ in that square; note that we do not exclude the possibility that two or more individuals use the same square. Initially, A at an individual's arrival location (i, j) is set equal to 1, and zero elsewhere. The values of A for each individual develop according to the individual's evolutionary strategy, which dictates the rules of habitat use in previously unfamiliar habitat, as specified below. Within one unit of time, individuals move through all the space they occupy, visiting every square in which A exceeds zero. Movement continues until the end of the settlement period, $t_{\max}$.

EXPLORATION OF EMPTY SPACE

The individual's strategy defines how it reacts to encounters with others. Before we proceed to describing these reactions, we specify how individuals encounter each other in the first place. In order to expand their initial territory of a single square (see above), explore new space and eventually meet other individuals, we assume an intrinsic tendency for an individual to increase the space that it uses. During each time unit, for each individual k, we take each location (i, j) in which $A(i, j, k, t)>0$, and assume that the surrounding squares $(i-1, j)$, $(i+1, j)$, $(i, j-1)$, $(i, j+1)$ all increase their value of A by the amount $\varepsilon A(i, j)$. The rate ε is equivalent to animals exploring unknown areas outside those with which they are familiar, in order to expand their home range or territory. To keep the model simple, we assume that ε is equal for all individuals, is fixed and does not evolve. We ensure that for each individual, A does not exceed 1, by resetting the value of A to 1 if the addition of ε takes it above this value.

EXPERIENCES WITHIN THE TERRITORY

We next describe the rules of habitat use that depend on an individual's strategy. We assume that during each visit to a square, individuals can have either an aggressive or a non-aggressive experience. Aggressive interactions between individuals occur wherever their space use overlaps. Thus, a time unit t is defined as being long enough such that individuals can be involved in multiple fights (in different squares) within one time unit. Our time unit thus corresponds to the time to independence, a concept that is used in home range studies to describe the time it takes an individual to use all of its home range (Swihart & Slade 1985, Swihart et al. 1988, Kernohan et al. 2001). Each individual may fight with several others, and/or several times with the same individual in different squares in the habitat area. During one time unit, a fight between individuals k_1 and k_2 will occur wherever $A(i, j, k_1, t) > 0$ and $A(i, j, k_2, t) > 0$. We make the assumption that fights occur wherever space use overlaps for simplicity, and to ensure that the resulting territories are spatially contiguous. Aggressive encounters (fights) can end with a win, a loss or a draw for each individual. We assume that all individuals have equal fighting abilities; following from this, we also assume that all fights end with a random outcome, such that a proportion d of fights will end with a draw. Fights that do not end with a draw end with a clear winner and loser, with equal probability of winning and losing for each individual: $(1-d)/2$.

A non-aggressive experience occurs when an individual k visits a square in which $A(i, j, k, t) > 0$, but does not encounter another individual. This occurs when a square used by the individual is not used by any other individuals (i.e. $A(i, j) = 0$ for all other individuals at time t). Thus, in total, there are four potential outcomes for an individual's visit to any given square: a win, a loss, a draw, or the individual can find the space empty. We assume that animals react in different ways to these four outcomes (dictated by their strategies), but a single individual always reacts in the same way to the same outcome; individuals are fixed in this aspect of their behaviour ('behavioural types', Sih et al. 2004). A reaction is an increase or decrease in A in each square, for each individual. After each time-step, a change in A of δ is added to or subtracted from each individual's A in each area, according to the outcome of the visit and the individual strategy. Again, we ensure that the value of A always remains between 0 and 1 by resetting the value to 0 if it becomes negative, and resetting to 1 if it exceeds this value. An individual's strategy is composed of its reaction to each of the four potential outcomes of a visit to a particular square.

STRATEGIES FOR TERRITORY ACQUISITION

There are potentially a large number of strategies, and considering every one is not feasible in our spatially explicit approach. We therefore consider four biologically interesting strategies, which differ in the way an individual using the strategy responds to the outcome of a fight, or finding a square empty. The strategies differ in their aggressiveness, defined by the behaviour of an individual after a fight: if an individual reacts positively to a fight (i.e. the outcome causes an increase in the occupancy value A), then the individual responds aggressively to that outcome.

Strategy 1: Cautious (Ca): For individuals using this strategy, fights have a negative effect on an individual's occupancy of the area, A, regardless of the outcome of the fight (that is, whether it won, lost or drew in the fight). Finding the space empty results in an increase in A (after Stamps & Krishnan 1999, 2001). Cautious is the least aggressive strategy we investigate.

Strategy 2: Common-sense (CS): Losing or drawing in a fight has a negative effect on occupancy, A, for common-sense individuals. Winning a fight and finding the space empty have a positive effect on A. This is similar to the 'winner-takes-all' strategy of early game theory models, and is a more aggressive strategy than cautious.

Strategy 3: Paradoxical (P): Positive effects on A result from losing or drawing in a fight; winning and finding the space empty have a negative effect. Individuals using the paradoxical strategy thus behave in exactly the opposite way to common-sense individuals. This strategy implies that intruders gain access to territories while the owners retreat. While deeply counterintuitive, it automatically emerges as a stable solution in many game theory models of contests over indivisible space (Maynard Smith & Parker 1976; Hammerstein & Parker 1982; Enquist & Leimar 1987; Mesterton-Gibbons 1992).

Strategy 4: Daring (D): Only losing a fight has a negative effect on A. All other experiences have a positive effect. This strategy is thus more aggressive than cautious or common-sense, as individuals are more likely to repeatedly encounter opponents.

Two strategies compete at one time, such that a proportion f of individuals use strategy S_1 and $(1-f)$ use S_2. We aim to investigate the fitness consequences of using different strategies (the calculation of fitness is defined below). We are interested in two basic events: whether a single individual using strategy S_1 can invade a population using S_2, and once this strategy has invaded, whether it can maintain a superior or equal fitness level as its numbers increase.

HOME RANGE SIZE AND EXCLUSIVITY

The home range of an individual is the total number of squares for which $A(i, j, k, t_{max}) > 0$, at the end of the settlement period, t_{max}. We also calculate the number of squares used exclusively by each individual. For individual k_1, this is the number of squares for which $A(i, j, k_1, t_{max}) > 0$, but $A(i, j, k_{2}\ {}_{N}, t) = 0$.

INDIVIDUAL FITNESS

The costs associated with fighting are represented by *c*. We assume that all fights carry equal costs, regardless of the outcome of the fight. Thus, the outcome of a fight itself rather than the costs experienced by an individual determines the individual's response to the fight. We make this assumption to make the model as symmetrical as possible, allowing us to investigate the paradoxical strategy as an alternative to the common-sense strategy. If we nevertheless find that paradoxical strategies cannot persist, the absence of paradoxical solutions in nature is better explained than had we made assumptions that possibly bias outcomes towards common-sense strategies.

We assume that there is no cost associated with finding a square empty of other individuals. Total contest costs for each individual, C_k, are calculated cumulatively at each time-step. An individual pays the costs associated with the outcome it experiences in each square in each time-step (see the Appendix). The benefits gained by each individual, B_k, are calculated at the end of the territory settlement period, $t_{\max}$. Each individual gains benefits B_k from each square it occupies, scaled by its occupancy, A, in that square, and the sum of A in the area for all individuals using the area. Thus, for individual k_1:

$$B_{k_1} = \sqrt{\sum_{i,j} \frac{A(i,j,k_1,t_{\max})}{\sum_{k=1}^{N} A(i,j,k,t_{\max})}}$$

The square root represents a diminishing returns relationship between the number of squares occupied by an individual and the benefits it gains from that area. This is a generally accepted relationship between the size of a territory and the benefits that can be gained from it. For a central place forager, for example, an increase in territory size increases the food available to the territory owner, but increases the time taken to transport it to the nest or retreat (Both & Visser 2003). For territories used purely for feeding, there is a maximum food intake above which fitness no longer increases (Gill & Wolf 1975; Schoener 1983).

The fitness of individual k, W_k, depends multiplicatively on the benefits gained (B_k) from the space it uses and the costs it pays (C_k) during fighting, scaled such that increasing costs lead to fitness approaching zero:

$$W_k = B_k e^{-C_k}$$

The multiplicative form indicates that territories are necessary to gain fitness, and an individual that uses none of the available space, gaining no benefits ($B = 0$) will have no fitness (but will remain extant), but neither will an individual whose costs of fighting are so high that survival is very improbable (e^{-C}). This form also ensures that fitness (a relative concept) never becomes negative. The negative exponential function indicates that each fight reduces the fitness benefits that can be gained by the same proportion. Strategy fitness W_S is estimated as the mean fitness of all individuals using strategy S after 20 iterations of the model.

EVOLUTIONARY STABILITY OF STRATEGIES

We investigated whether a population of each of the strategies is stable against invasion by a single mutant individual using one of the alternative strategies (*f* = 1/*N*). We investigate whether populations are stable against mutants under different levels of costs (*c*) and population density (*N*). The details of the algorithm are provided in the Appendix. If a strategy is susceptible to invasion by a mutant, we can investigate whether the mutant strategy gains higher or lower mean fitness than the population when its numbers increase (*f* = 0.5). Here we consider only a single generation: a potentially fruitful avenue of further research would be to allow the frequency of individuals using a certain strategy to evolve over many generations. The model also allows us to compare the fitness of populations of a single strategy, and the territories they gain. Since our model is stochastic, the stability of a population has to be interpreted in the following conservative way: A mutant is able to invade a population if its fitness is equal to or greater than the mean strategy fitness of the population (solid lines in figures 5.3 and 5.4, 'Y' in table 5.2). A mutant cannot invade a population if the population has greater mean fitness than the mutant (dashed lines in figures 5.3 and 5.4, 'x' in table 5.2). Invadability was investigated using paired t-tests; *p*-values were Bonferroni corrected (Rice 1989) within a set of parameter values. Under some parameter values, either the mutant, or the population, or both, gain fitness of zero (when both the invader and the population gain zero fitness, it shown by a dotted line in figures 5.3 and 5.4), and thus cannot invade or resist invasion.

PRELIMINARY SIMULATIONS

Preliminary investigations of the simulation model revealed that spatially contiguous territories were established for each individual, and that 100 time-steps ($t_{max} = 100$) were sufficient for space use to approach equilibrium. At equilibrium, when space was divided, there was variation between individuals in the number of squares used, even when all individuals were equal and using the same strategy.

Results

POPULATION PERFORMANCE

We first compare the performance of strategies in isolation from each other. When all individuals in the population are using the same strategy, a population of cautious individuals displays the highest mean fitness, followed by populations of common-sense individuals. Populations of daring (D) and paradoxical (P) individuals gain very low fitness, much lower than that of cautious (Ca) and common-sense (CS) individuals when the costs associated with fighting are low (figure 5.1, open bars). This pattern also exists when the costs of fighting are intermediate, although fitness values are lower when costs are higher, and common-sense does not differ from paradoxical and daring strategies (figure 5.1, filled bars). At high fighting costs, fitness values are very low for all populations (not shown). Thus, in a 'good for the species' point of view that ignores invasibilities, the least aggressive strategies that show avoidance behaviour perform best.

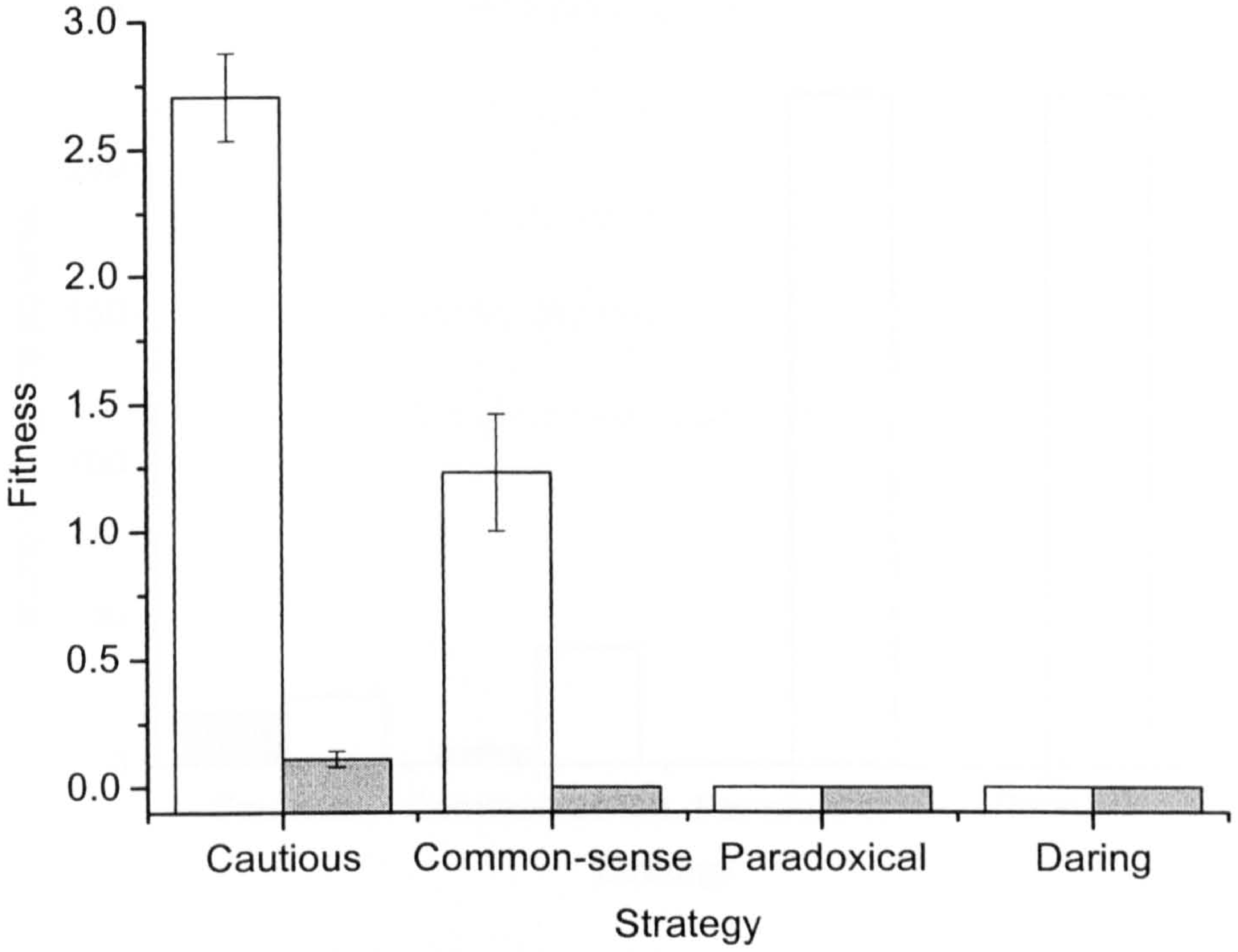


Figure 5.1: Mean (± SD) fitness gained by individuals using each strategy when all individuals in the population are using the same strategy, for low costs ($c = 0.0001$, open bars: ANOVA: $F_{3,76} = 1613.15$, $p<0.001$, Tukey's B post-hoc test revealed that Cautious (Ca) and common-sense (CS) strategies differ from one another, and also differ from the paradoxical (P) and daring (D) strategies) and intermediate costs ($c = 0.001$, filled bars, ANOVA: $F_{3,76} = 223.54$, $p<0.001$. Tukey's B post-hoc test revealed that P, D and CS have similar fitness, but C gained higher fitness). Parameter values used: $N = 10$, $a = 15$, $d = 0.8$, $\delta = 0.1$, $\varepsilon = 0.1$, $t_{\max} = 100$. The model was run 20 times for each strategy.

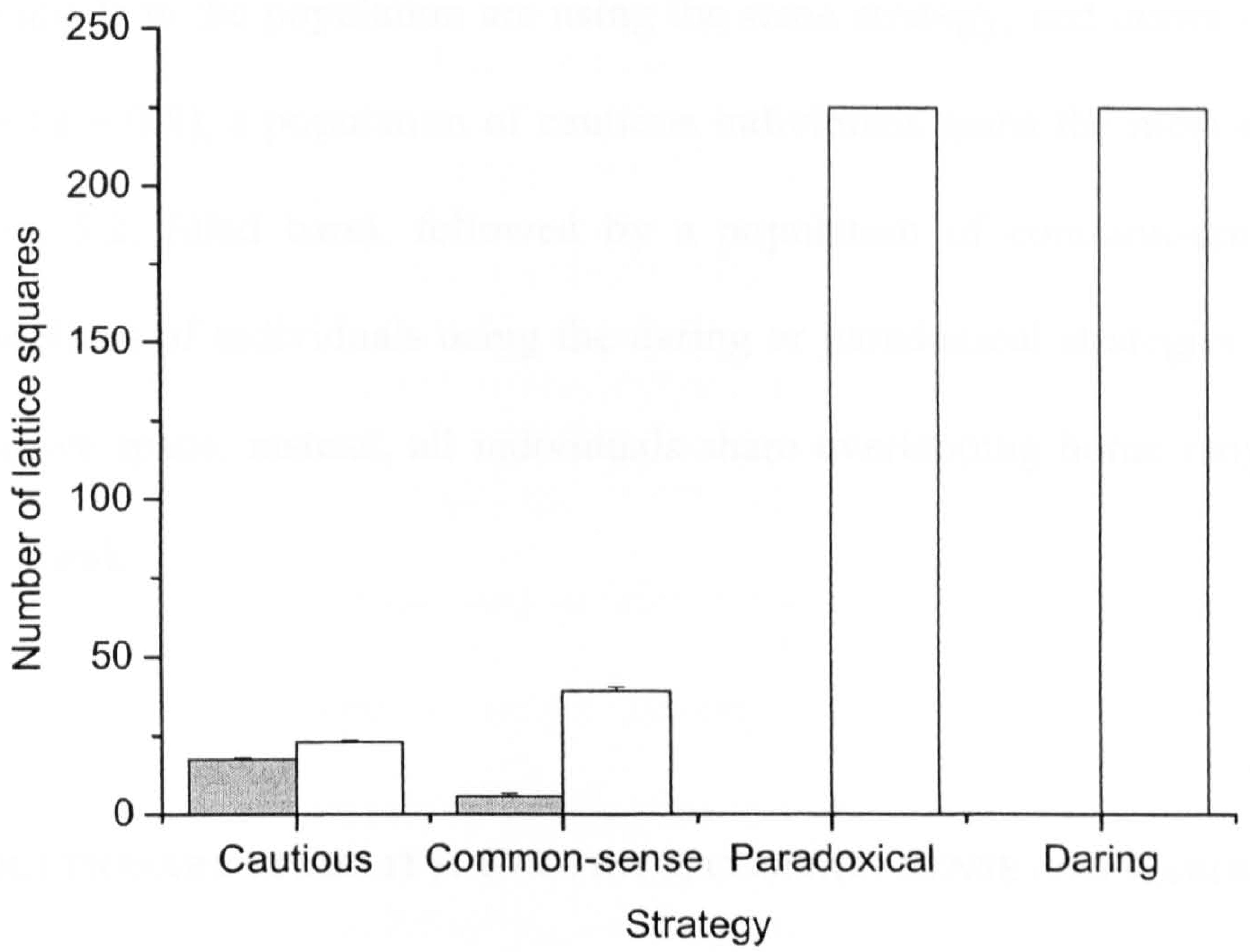


Figure 5.2: Mean (± SD) number of lattice squares occupied exclusively by one individual (filled bars; ANOVA: $F_{3,76} = 4114.26$, $p<0.001$, Tukey's B post-hoc test revealed Ca > CS > P and D, abbreviations as figure 5.1) and total number of squares used by each individual, including those occupied exclusively (open bars; ANOVA: $F_{3,76} = 431010.65$, $p<0.001$. Tukey's B post-hoc test revealed P and D > CS > Ca), when all individuals in the population use the same strategy. Parameter values used: $N = 10$, $a = 15$, $d = 0.8$, $\delta = 0.1$, $\varepsilon = 0.1$, $c = 0.0001$, $t_{\max} = 100$. The model was run 20 times for each strategy.

An important question to ask in a discussion of territoriality is whether the strategies under consideration can divide space and form stable territories. When all individuals in the population are using the same strategy, and draws occur relatively often ($d = 0.8$), a population of cautious individuals gains the most exclusive space (figure 5.2, filled bars), followed by a population of common-sense individuals. Populations of individuals using the daring or paradoxical strategies do not get any exclusive space, instead, all individuals share overlapping home ranges (figure 5.2, open bars).

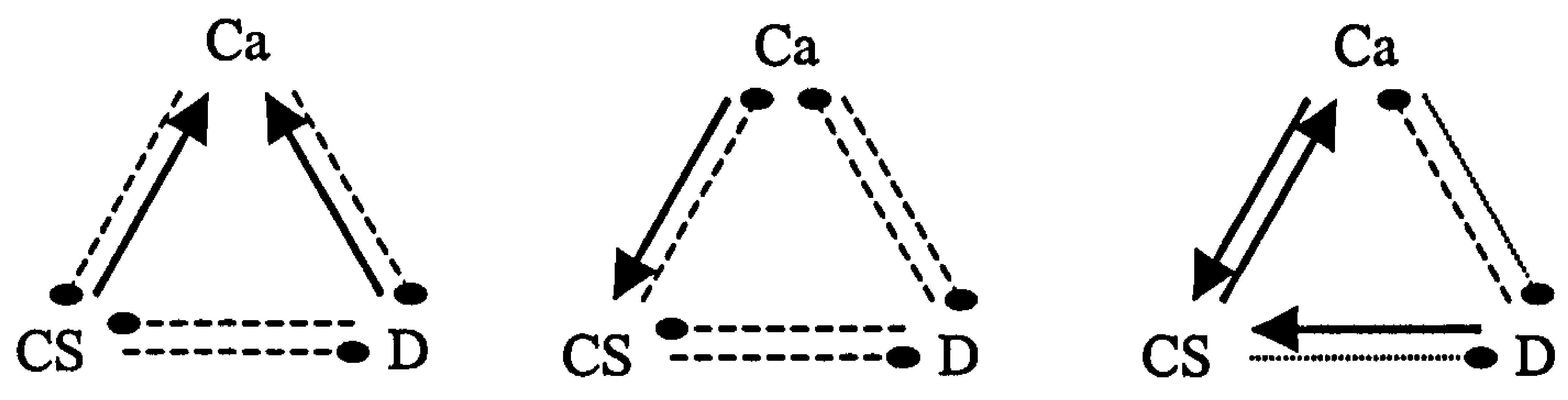
EVOLUTIONARY STABILITY: CAUTIOUS, COMMON-SENSE AND DARING

In an evolutionary setting, the important question is whether a population using a particular strategy is stable against invasion by a single mutant individual using a different strategy, and how this is affected by different costs of fighting and population density. We compare three of our four strategies, cautious, common-sense and daring, representing increasing aggressiveness in individuals using the strategies. We will consider the success of the paradoxical strategy in a separate section below.

Increasing the costs of fighting alters the ability of strategies both to invade and resist invasion by other strategies (figure 5.3). At low costs of fighting (c=0.0001), cautious strategies are unable to invade or resist invasion by either of the more aggressive strategies, but as the costs increase to an intermediate level ($c = 0.001$), cautious is able to invade a common-sense population, and resist invasion by both common-sense and daring strategies. When the costs of fighting are high ($c = 0.005$), cautious continues to invade common-sense, but can once again be invaded by common-sense. This is due to the extremely low fitness gained by individuals both types of individuals when the costs of fighting are high.

Common-sense populations are resistant to invasion when the costs of fighting are low, but increasing costs means that they can be invaded, first by the cautious strategy (intermediate costs) and then by the daring strategy (high costs; figure 5.3). Both common-sense and cautious strategies are unable to invade a daring population regardless of the costs of fighting. When fighting costs are high, fitness can decline to zero for both the invader and invaded strategy. Daring is a relatively ineffective strategy as an invader: a single daring individual can only invade cautious populations when the costs of fighting are low, and common-sense populations when the costs are high. It is, however, stable against invasion by both common-sense and cautious individuals, regardless of the costs of fighting.

Increasing the number of individuals present in the habitat area also influences whether individuals using one strategy can invade a population using a different strategy (figure 5.4). In general, increasing the density of individuals increases the likelihood that the more aggressive strategies are successful as invaders. At low population density ($N = 5$), cautious can invade common-sense populations, but all other invasions are unsuccessful. Increasing the density to $N = 10$ results in cautious populations no longer being stable against invasions from common-sense and daring individuals, and further increasing to $N = 15$ means that common-sense populations can now be invaded by daring individuals, whereas under lower population densities these populations are stable against invasion.



Costs: low intermediate high

Figure 5.3: The effect of increasing the costs of fighting on the ability of an individual using each strategy to invade populations using each alternative strategy. Solid arrows indicate that an invader using the strategy at the foot of the arrow is able to invade a population of individuals using the strategy at the head of the arrow. Dashed lines indicate that invasion of the population at the is not possible, and dotted lines indicate that both the invader and the population gain zero fitness when invasion into the population at the is attempted, based on 20 runs for each invasion. Abbreviations used: Ca = cautious, CS = common-sense, D = daring. Parameter values used: low costs: c = 0.0001, intermediate costs: c = 0.001, high costs: c = 0.005, N=10, a=15, d=0.8, $t_{\max}$=100, δ=0.1, ε=0.1,

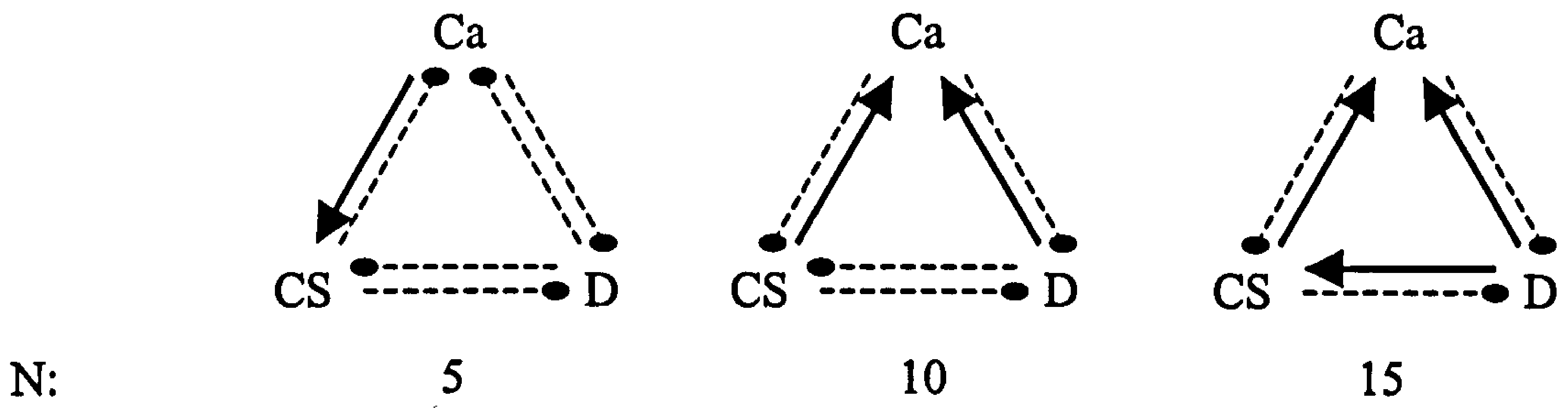


Figure 5.4: The effect of increasing population density on the ability of individuals using each strategy to invade populations using each alternative strategy, based on 20 runs for each invasion. Abbreviations and arrows figure 5.3. Parameter values used: $c = 0.0001$, $a = 15$, d=0.8, t=100, δ=0.1, ε=0.1

LONG TERM INVASION POTENTIAL

Once an individual using a different strategy has invaded a population, it may reproduce and increase in number. Thus, we can investigate the effect of an increased frequency of the invading strategy (increasing f of strategy S_1). We chose as an example to investigate the effect of equal numbers of each of the two strategies present in the population ($f = 0.5$), for one of the population densities considered above ($N = 10$). When the daring strategy is present in the population at $f = 0.5$, those individuals always gain higher mean fitness than the cautious or common-sense individuals they share the habitat with (table 5.1). This suggests that even if common-sense or cautious individuals are able to invade a daring population, their numbers are unlikely to increase.

Table 5.1: Relative fitness when strategies are equally common in the population, showing the strategy that gains higher fitness, for different levels of fighting costs. Abbreviations used: Ca = cautious, CS = common-sense, D = daring. Low costs: $c = 0.0001$; intermediate costs: $c = 0.001$; high costs: $c = 0.005$. Other parameters used: $N=10$, $a = 15$, $d=0.8$, $t=100$, $\delta=0.1$, $\varepsilon=0.1$, 20 runs for each parameter and strategy combination.

Strategy Pair		Costs		
		Low	Intermediate	High
Cautious	Common-sense	CS	CS	Ca
Cautious	Daring	D	D	D
Common-sense	Daring	D	D	D

In populations consisting of 5 individuals using the common-sense strategy and 5 individuals using the cautious strategy, the individuals using the common-sense strategy gain highest fitness when the costs of fighting are low ($c = 0.0001$) or intermediate ($c = 0.001$), but the cautious individuals gain higher fitness when the costs of fighting are high ($c = 0.005$). At low fighting costs, a common-sense individual can invade a cautious population (figure 5.3), and its fitness is also higher when it makes up 50% of the population (table 5.1). At intermediate costs, a cautious individual can invade a common-sense population (figure 5.3), but it gains lower fitness than the common-sense individuals when they are equal in number (table 5.1). When fighting costs are high, both cautious and common-sense individuals can invade populations of the other strategy (figure 5.3), but at 50%, the cautious strategy prevails (table 5.1). Thus, under high fighting costs, cautious individuals have the potential to invade common-sense populations over a longer time period, but common-sense individuals do not have the potential to invade cautious populations.

THE IMPORTANCE OF DRAWS - COMMON SENSE AND PARADOXICAL STRATEGIES

We now investigate whether an individual using the common-sense or paradoxical strategy can invade populations using other strategies, when draws occur either commonly ($d = 0.8$) or less commonly ($d = 0.2$). When draws are common, there is a clear difference between the common-sense and paradoxical strategies: a single paradoxical individual can invade a daring population, but a common-sense individual cannot (table 5.2). However, when draws are less common, both common-sense and paradoxical strategies can invade daring populations, and also invade populations of each other, and in this way, behave identically (table 2).

We also compare the fitness and territories gained by common-sense and paradoxical populations (i.e. the population performance, see above), and investigate the effect of changing the probability of a draw. When draws are common ($d = 0.8$), the common-sense strategy gains more exclusive space (figure 5.2) and higher fitness than paradoxical when the costs of fighting are low ($c = 0.0001$; figure 5.1). When draws occur only less frequently ($d = 0.2$), the fitness of common-sense individuals decreases (mean fitness ± 2 S.E = $1.46*10^{-7}$± $3.57*10^{-9}$, d = 0.2, other parameter values as fig. 1). Common-sense territories decrease from 5.65 ± 4.226 (mean ± 2 S.E) exclusive squares when draws are common, to no exclusive squares when draws are less common (d = 0.2, other parameter values as fig. 2). Paradoxical individuals gain no exclusive space in either case. Thus, when draws occur less commonly, common-sense individuals become much more similar to paradoxical individuals than when draws are a common outcome of fights.

Table 5.2: The ability of common-sense (CS) and paradoxical (P) strategies to invade populations using each alternative strategy, for two different probabilities that the fight ends without a clear winner and loser. Abbreviations as table 5.1, plus: Y = mutant can invade, x = mutant cannot invade. Parameter values used: c = 0.001, N=10, a=15, δ=0.1, ε=0.1, t=100, 20 runs for each invasion.

	$d=0.8$		$d=0.2$	
Mutant Population	CS	P	CS	P
C	x	x	x	x
CS	-	x	-	Y
D	x	Y	Y	Y
P	x	-	Y	-

Discussion

Our modelling clearly shows that spatial division is a more complicated issue than a strategy's success in contests over one resource item would predict. Models such as hawk-dove games (Maynard Smith & Price 1973; Grafen 1979; Houston & McNamara 1991; Mesterton-Gibbons 1992; Crowley 2000), concentrate on what happens when two contestants have already met, and a fight ensues. Other approaches assume that space can only be gained as the result of winning contests (Maynard Smith 1982, Pereira et al. 2003). This ignores the possibility that individuals may gain space simply by being 'cautious', that is, be deterred from space that is contested, and seek other empty spaces instead (Stamps & Krishnan 1995, 1998, 1999, 2001). To find out the success of such a strategy, it is necessary to realise that a strategy can have positive fitness even if it loses ownership of one particular location; in other words, a spatially explicit treatment is needed.

Morrell and Kokko (2003; **chapter 4**) showed, in a simple one-dimensional three-compartment model, that 'cautious' type strategies can be successful if the value of monopolisation of a resource item is low, for example, when the contest is over a moderately small expansion of a territory, rather than territory ownership itself. Lewis and Moorcroft (2001) have likewise shown, in a model inspired by scent-marking wolf packs, that strategies that yield minimal conflict with neighbours can be evolutionarily successful. Here we have shown that this idea holds in a general setting, with interactions that resemble hawk-dove encounters of early game theory models, but interpreted in a spatially explicit framework that allows assessment of whether territories form, validating some of our earlier findings (Morrell & Kokko

2003; **chapter** 4). When fighting costs are high relative to the value of the resource, evolutionarily stable behaviour generates well-defined, exclusive territories, either through 'cautious' or 'common-sense' behaviour, due to avoidance following aggressive encounters. By contrast, if costs of fighting are low compared to resource value, territoriality breaks down and evolution proceeds to the formation of large, overlapping home ranges, where avoidance of fight locations does not occur. That increasing costs favour strategies that avoid conflict is well known from early game theory (Maynard Smith & Price 1973; Maynard Smith & Parker 1974; Parker & Knowlton 1980), and costly conflicts can lead to the evolution of exclusive territories in ant colonies (Adler & Gordon 2003).

In our model, high fight costs lead to the formation of territories through avoidance behaviour. However, once territories are established, interactions between neighbours tend to be of low intensity and low cost, compared to interactions between territory owners and intruders (the 'dear enemy phenomenon'; Getty 1987; Ydenberg et al. 1988; Temeles 1994). Such reduced aggression emerges as the result of increasing familiarity between individuals that interact frequently (e.g. Morris et al. 1995; Höjesjö et al. 1998; Utne-Palm & Hart 2000), after the settlement period considered in the model. In the case of overlapping home ranges and very low fight costs, one should note that the terms 'fighting costs' and 'aggressive' may become misleading; a better interpretation of a 'fight' in such a case is a low-cost interaction between individuals who share space, e.g. through resource depletion without overt aggression. The evolutionarily stable behaviour in such a case is the most aggressive behaviour, 'daring', and it simply describes any non-territorial species, for which the costs of sharing space with conspecifics are not sufficient to deter any individual from using any particular region of the area, and which responds in an optimistic way to interactions with others.

We assume that all fights carry the same cost, regardless of the outcome. In some cases, winners and losers pay equal costs (Smith & Taylor 1992). In others, losers incur higher costs than winners (Neat et al. 1998a), while in some cases, the energetic cost of winning may even exceed that of losing (Hack 1997). One might expect an individual to respond more strongly to fights that carry greater costs, for example, an individual using a cautious strategy might be less likely to return to a location in which it has suffered high fight costs (perhaps through losing) than one in which it has suffered lower costs because it won the fight (Stamps & Krishnan 2001). Our assumption that all fights are equally costly and have an equal magnitude of effect allows us to investigate the effect of the fight outcome itself rather than a response to the costs paid as a result of the fight.

In addition to investigating the costs of fighting, our spatially explicit treatment also allows us to consider effects of population density. Clearly, being 'cautious' only pays if there is sufficient empty space available to be won. In denser populations, common-sense strategies can prevail, and in the densest populations, territoriality breaks down. This pattern fits in well with the ideas of economic defensibility of territories (Brown 1964; Adams 2001; Both & Visser 2003), and with game theory findings that increasing density favours individuals that act more aggressively (e.g. Parker & Knowlton 1980; Mesterton-Gibbons 1992).

The costs and benefits of territory maintenance have commonly been found to change with intruder pressure (e.g. Iguchi & Hino 1996; Praw & Grant 1999; Adams

2001), and there is some evidence to suggest that population density affects territorial behaviour. In lizards, individuals gain more exclusive home ranges at low densities than at high densities (Stamps & Krishnan 1998). In juvenile salmonid fish, territorial behaviour occurs only at low population densities; at high densities, individuals share space, and little aggression occurs (Kallenberg 1958). However, in the funnel-web spider *Agelenopsis aperta*, the costs of maintaining territories in habitats near saturation is higher than that in habitats where space is more readily available, but territorial behaviour does not appear to vary (Riechert 1979, 1981), perhaps due to external constraints such as gene flow (Hammerstein & Riechert 1988).

A limitation of our model is that population density is a parameter that can take different values, rather than be a consequence of the population dynamics that the individual behaviour generates (Eshel & Sansone 1995; Mylius & Diekmann 1995; Kokko & Lundberg 2001). However, our results are consistent with other work in this area. Considering territorial turnover in a setting with a fixed number of breeding spots, Dunham et al. (1995) showed that a non-aggressive 'waiting' strategy prevailed when injury rate was high and if territory owners had a high death rate. Both factors have the effect of lowering population density, lending support to the idea that life histories that lead to much vacant space in the environment allow spatial strategies with relatively non-aggressive behaviour to prevail in a population, with ownership fully respected. At a higher density individuals may get more 'desperate' (*sensu* Grafen 1987).

ON THE ABSENCE OF PARADOXICAL STRATEGIES IN NATURE

Theoretical models often produce paradoxical solutions to contests over the acquisition of indivisible space (Maynard Smith & Parker 1976; Hammerstein & Parker 1982; Maynard Smith 1982; Enquist & Leimar 1987; Mesterton-Gibbons 1992), so that owners retreat when challenged by intruders. Such solutions are found when asymmetries in resource holding potential are small or absent (RHP; Parker 1974a), yet they rarely occur in nature (but see Burgess 1976; Fernet & Smith 1976; Peeke et al. 1998). Our model provides a novel explanation for the absence of paradoxical strategies in nature that does not rely on RHP asymmetries. If a large proportion of fights end without a clear winner or loser (Bleistein et al. 1994; Stamps & Krishnan 1994a, b, 1997, 1998; Adams 1998; Stamps 1999; Draud et al. 2004), then the common-sense strategy wins over the paradoxical alternative because it responds more adaptively to draws. The common-sense strategy behaves cautiously after a draw. The paradoxical strategy's response resembles that of 'daring', with the associated benefits and costs: it can invade 'daringly', but is not able to form stable territories and persist on its own if repeated encounters are costly.

Had we defined the paradoxical strategy as different from the common-sense one with respect to responses to wins and losses only, we would not have found the above asymmetry in the outcome (this would correspond to swapping the labels 'win' and 'loss', without paying attention to the biological meaning). Under such a definition, any fitness difference between the paradoxical and common-sense strategies would have to arise through other mechanisms (e.g. Mesterton-Gibbons 1992, Morrell & Kokko 2003). However, our fitness comparisons rely on cognitive 'rules of thumb': behavioural mechanisms dictate that one is likely to find correlated responses to situations that resemble each other. Since both 'loss' and 'draw' entail not acquiring the desired resource, swapping the response to one outcome is likely to influence the decisions made in another situation too.

CONCLUSIONS

To summarise, our model has shown that it is possible to bridge the gap between spatially explicit, two-dimensional, mechanistic models of territory formation and adaptive models of animal conflict. Our model also shows that avoidance of high fighting costs easily results in solutions where individuals settle and agree on boundary locations even though some individuals end up with much smaller spaces than others — despite every individual being equal in our model. In our model, the space was uniform, with no habitat gradients or landmarks that could serve as territorial boundaries.

An interesting case for future development is the inclusion of landmarks: arbitrary features of the landscape that can be used as conventions dictating the boundaries of territories, and therefore reduce the frequency of aggressive encounters (Eason et al. 1999; LaManna & Eason 2003; Mesterton-Gibbons & Adams 2003). In a two-player setting with a one-dimensional (linear) territory, landmark use has been found to be a stable convention (Mesterton-Gibbons & Adams 2003), even if it significantly reduces territory sizes for the owner of the smaller territory. Investigating the limits of such conventions in a spatially realistic setting, and examining its population consequences, would be a fruitful avenue of further research.

Appendix: Model of spatial division

The following steps outline the simulation model of spatial division.

1. Define the strategies and other parameters used in the model. Select the two strategies S_1 and S_2 to be tested against each other.

2. N individuals are each allocated one of the two selected strategies. The number of individuals allocated each strategy is determined by the parameter f. For a single invading mutant, $f = 1/N$. The first fN individuals are allocated strategy S_1, and the remainder, strategy S_2

3. The N individuals arrive in a grid of squares measuring a squares by a squares. The grid of squares is wrapped such that each square has exactly 4 neighbouring squares. The initial location of each individual (i, j) is determined randomly, and is independent of the location of all other individuals.

4. A for each individual (k) is set to 1 in the initial location square (i, j), such that $A(i, j, k, t_1) = 1$. A in all other squares is set to zero.

5. For each individual, A in all squares surrounding its initial location increase by εA (which in this case is equal to ε).

6. Each individual uses all squares in which $A(i, j, k, t) > 0$. For each individual, k_1 to k_N, we compare the location identities of all squares in which $A(i, j, k, t) > 0$ with the location identities of all other individuals.

7. For each possible pair of individuals, we record the location where both $A(i, j, k_1, t) > 0$ and $A(i, j, k_2, t) > 0$. At this location, a fight takes place.

8. The outcome of the fight is determined randomly, with a probability d that the fight ends in a draw. If a number drawn from a random number distribution is less than $(1-d)/2$, we record that individual k_1 won the fight, and individual k_2 lost. If the random number is between $(1-d)/2$ and d, we record a loss for individual k_1 and a win for individual k_2. Otherwise, we record a draw for both individuals. This step is repeated for all possible pairs of individuals in all locations where both $A(i,j, k_1, t) > 0$ and $A(i,j, k_2, t) > 0$.

9. For each fight, the costs to the each of the participants is recorded, and added to any existing costs already paid by the individual from other fights in the same or previous time-steps.

10. As a result of the outcome of fights, $A(i, j, k, t)$ changes in accordance with the individual strategy, by a value δ. For each fight recorded above, we determine how A will change as a result of the value of δ and the strategy used by the individuals involved in that fight. These changes (some of which are positive and some negative) are recorded for each square for each individual.

11. If there is no fight in a particular square for a particular individual, A changes in accordance to their response to finding the space empty. Combining steps 10 and 11 gives a change in A for each square, for each individual.

12. When all the changes as a result of the fights have been recorded, they are added to the original A value for each square. Any A values which then exceed 1 or are below zero are set to 1 and 0 respectively.

13. At each location (i, j) in which $A(i, j, k, t) > 0$, the surrounding squares $(i-1, j)$, $(i+1, j)$, $(i, j-1)$, $(i, j+1)$ all increase their value of A by the amount $\varepsilon A(i, j)$.

14. Steps 6 to 13 are repeated for t_{max} times. After this, the simulation ends.

15. At the end of the simulation, individual fitness, home range size and number of squares used exclusively are calculated, and grouped according to the strategy used by the individual. Strategy means are then calculated and collected.

16. The entire simulation is repeated 20 times.

CHAPTER 6

ARE BEHAVIOURAL TRADE-OFFS ALL THEY SEEM?

COUNTER-INTUITIVE RESOLUTION OF THE CONFLICT BETWEEN TWO BEHAVIOURS

Abstract

The understanding of trade-offs between behaviours is fundamental to the study of animal behaviour. Individuals may often be faced with the choice of which of two mutually incompatible behaviours to perform. Here, I present a model investigating the trade-off between two behaviours, where one of the behaviours is crucial to the success of the other. I illustrate the results with examples, considering particularly a trade-off between territorial defence and courtship. I investigate how the ability of an individual to perform the behaviours changes the time or energy allocated to each behaviour. Intuition suggests that the time invested in performing a behaviour should decline as the individual's ability to perform the behaviour increases. Explicit, quantitative modelling suggests that this is not always the case. Instead, we see a pattern where investment in one of the behaviours at first increases and then decreases as the ability to perform the behaviour increases. This finding has implications for the empirical study of trade-offs between behaviours, since it could appear that individual ability has no effect on the trade-off under consideration. I discuss potential methods for distinguishing whether time allocation changes in a counter-intuitive, non-monotonic way with increasing individual ability, or whether there is indeed no effect.

Introduction

Animal behaviour can be thought of as the outcome of a series of trade-offs between the costs and benefits associated with performing various actions. A central tenet of behavioural ecology is that animals are expected to maximise net benefits, leading to optimal behaviour (but see Roff 1992). The study of trade-offs is thus fundamental to our understanding of animal behaviour. Behavioural trade-offs can occur within a single behaviour, for example, the decision to defend a territory involves trading off the costs of defending territories against the benefits gained from monopolisation of the resources they contain (e.g. Hixon 1980; Schoener 1983; reviewed in Adams 2001). Behavioural trade-offs may also occur between two or more behaviours, when individuals are faced with a choice of mutually incompatible behaviours they can perform.

When presented with the option of selecting one of two behaviours to perform, the optimal behaviour for an individual will depend on the fitness consequences of different potential actions. However, if the benefits of performing one behaviour were significantly greater than the benefits of the other, one would imagine that an individual would abandon the second behaviour in favour of the first. Here, I present a general model that investigates the trade-off decision faced by an individual when allocating time or energy to two behaviours. Specifically, I ask how much of their available time (or energy resources) individuals should invest in each activity when their ability to perform the necessary behaviours varies. Intuition suggests that as an individual becomes increasingly able to successfully perform a behaviour, the time it needs to invest in doing so would decrease, as its efforts are likely to be more effective, allowing more time to be invested in the other activity.

As illustrative examples, I discuss potential trade-offs between territory defence and courtship of potential mates, and between these behaviours and predator avoidance. In territorial animals, courtship and defence behaviours may be in conflict (i.e. they cannot be performed simultaneously). Empirical studies investigating the question of a trade-off between territory defence and mate courtship have found that both sticklebacks (*Gasterosteus aculeatus*; Sevenster 1961; Wilz 1972; Candolin 1997) and beaugregory damselfish (*Stegastes leucostictus*; Santangelo et al. 2002) invest less time or effort in courtship when both potential mates and competitors are present compared to when only potential mates are present. This suggests that the two behaviours cannot be performed simultaneously and a decision must be made as to how to allocate time or energy to these behaviours.

In this example, the fitness trade-off could be as follows: if the benefits gained from retaining a territory exceed those gained from a given mating opportunity (e.g. if territories are scarce and carry long term benefits), a male should ignore a potential mate and concentrate instead on ensuring his territory is adequately defended. Alternatively, if the benefits from gaining a mating are significantly greater than the benefits of defending a territory, one would imagine that territorial males would abandon defence in favour of courting a female. If, however, territories are essential for breeding, abandoning territory defence in favour of courtship would bring no benefits.

Both territorial defence and mate searching can increase exposure to predators (Daly 1978; Alatalo et al. 1988a; Reynolds & Gross 1990; Crowley et al. 1991; Pruett-Jones 1992), and have been found to alter as the risk of predation increases (e.g. Berglund 1993; Hedrick & Dill 1993; Godin & Briggs 1996; Jennions & Petrie 1997; Candolin & Voigt 1998; Koga et al. 1998). For example, courtship displays involving conspicuous behaviours are reduced when courting individuals perceive a greater risk of predation (e.g. Endler 1987; Sih et al. 1990; Fuller & Berglund 1996; Godin 1995). Thus, territorial defence behaviour, courtship and mate search behaviour appear to trade-off both with each other and with predator avoidance and vigilance behaviour. If we imagine a population in which predation risk is intense, and vigilance is thus very important, it is clear that abandoning vigilance in favour of defensive or courtship behaviours would have no benefits: an individual devoting all its time to courtship would be unable to avoid predation, and would be quickly eaten. The same effect is not true of the reverse, however. An individual choosing to be vigilant rather than court mates or defend a territory would survive to the following breeding season, where it would have the opportunity to mate again. Under such conditions, the study of trade-offs may become more complex, compared to a situation where the behaviours have equal importance.

In a quantitative genetic model of life-history trade-offs, Worley et al. (2003) showed that trade-offs can be masked when the allocation of resources to different traits occurs in a 'nested' fashion, i.e. when a fraction of resources is allocated to one trait and the remainder subdivided between other traits (Worley et al. 2003). In a behavioural context, Houston et al. (2003) showed that differences in individual quality can produce counter-intuitive patterns of optimal behaviour, when fitness is a product of the benefits gained from the two behaviours (and they are therefore, in a sense, of equal importance). Here, I incorporate the possibility that behaviours are nested: it is crucial that one of the behaviours (for example, vigilance or territorial defence) is performed before the other (e.g. courtship) can be successful. Fitness can result from performing the more crucial behaviour (vigilance) in the absence of the other, but not vice versa, or from a combination of both. Additionally, I incorporate the possibility that an individual may not be equally ranked in its ability to perform two behaviours. For example, the most dominant individuals may not necessarily be the most attractive (Qvarnström & Forsgren 1998). The results of the model suggest that the relationships between two behaviours are not as simple the verbal arguments above might imply. Given the counter-intuitive patterns suggested by this and other models, it may (erroneously) appear that a trade-off between two behaviours is not affected by ability in a particular study system. Thus, I make suggestions as to how it would be possible to determine whether there is indeed no effect, or the pattern is counter-intuitive due to the interaction of differences in quality (ability to perform a certain task) and allocation.

Model

The model assumes that an individual animal has a certain amount of time or energy that is not devoted to maintenance activities such as resting or foraging, and that this is fixed and does not vary between individuals. This time or energy (not used in maintenance activities) can be divided between the mutually exclusive behaviours A and B. I assume that both behaviours can potentially be performed, but that B cannot be successful in the absence of *A*, although *A* can be successful in the absence of *B*, and ask how an individual should divide its available time between them. Examples of the behaviours to which the model applies are found in table 6.1.

An individual spends a proportion of time t_A performing behaviour *A*, leaving a proportion $t_B=1-t_A$ available to invest in behaviour *B*. The time invested in performing a behaviour directly affects the probability that the behaviour will have a successful outcome. An individual investing nothing in behaviour *A* will gain zero benefits from that behaviour, while an individual investing all its time in behaviour *A* will obtain maximum benefits from it. An individual which is effective at performing behaviour *A* will need to invest less time in doing so than one who is less effective to gain the same benefits, and is likely to obtain higher maximum benefits. For example, in the context of a trade-off between courtship and defence, a territory owner that was able to repel intruders quickly would need to spend less time in territory defence than one that spent longer in aggressive interactions (all intruders are considered equal in the model), and would be more successful in retaining the territory. A curvilinear function with diminishing returns gives an appropriate description of this relationship between time or energy invested in a behaviour, and probability that the outcome of the behaviour is successful. Therefore, given an individual's current investment in behaviour *A*, t_A, the probability of a successful outcome from that behaviour, p_A, is well described by the simple expression:

$$p_A = \delta_A\left[\left(\frac{1}{1+e^{-\alpha t_A}}\right)-0.5\right] \qquad (1)$$

where α describes the ability of an individual performing behaviour A; it takes values in the range 1 to $\alpha_{\max}$, where 1 describes low ability and $\alpha_{\max}$ describes high ability in the individual. The parameter δ_A and the constant 0.5 serve to scale the benefits between zero and 1, where $\delta_A = 1+(\alpha/\alpha_{\max})$, such that the highest quality individuals are most successful. The probability of a successful outcome from performing behaviour B, p_B, is well described by an analogous expression:

$$p_B = \delta_B\left[\left(\frac{1}{1+e^{-\beta t_B}}\right)-0.5\right] \tag{2}$$

where β describes the ability of the individual to perform behaviour B. β takes values from 1 to $\beta_{\max}$, 1 describes a low ability to perform behaviour B, and $\beta_{\max}$ a high ability. Again, $\delta_B = 1+(\beta/\beta_{\max})$. For example, an attractive male or one able to easily perform necessary courtship behaviours should need to spend less time persuading a female to mate with him than an unattractive male or one who is less able to perform the courtship behaviours, given that all females are equally receptive to courtship.

The model applies to situations where behaviour A is of value in the absence of B, but B has no value without A. For example, if territories are a prerequisite to breeding, courtship (B) has no value in the absence of territory defence (A) as the male would lose his territory and thus not be able to breed successfully. Individual fitness, W, depends on the probabilities of successful outcomes of the two behaviours. Some fitness is gained when both behaviours are performed successfully (for example, when a territory owner successfully retains the territory and attracts a mate to breed), and additional fitness is gained when the individual successfully performs only behaviour A (for example, when the individual retains the territory but fails to attract a mate; see also table 6.1 and the Discussion for examples). Thus:

$$W = p_A p_B + p_A(1 - p_B)\gamma \tag{3}$$

The second component of fitness is scaled by the relative benefits of performing only behaviour A, γ. The value of γ is fixed in the population and does not vary between individuals. High values of γ (close to 1) indicate that the fitness benefits of performing only behaviour A are relatively high, and low values (closer to zero) suggest that behaviour A is of little worth unless combined with behaviour B. In the courtship versus defence example, γ describes the value of owning a territory without attracting a female to breed, an aspect of species ecology that does not vary between individuals or territories. High values of γ suggest that territories have high value in the absence of successful reproduction (for example, they may be used for feeding and thus be essential for survival). Low values of γ suggest that territories may be solely for breeding purposes, and thus have little value if the owner fails to attract a mate.

A individual's optimum investment in behaviour A (t_A*) versus B (t_B*) is the proportion of time invested in behaviour A, t_A, that maximises his fitness, W, for a given set of parameter values. Optimum investment was calculated using a computer simulation as analytical solutions were not available.

Table 6.1: Examples of trade-offs to which the model applies, and descriptions of the parameters for each example.

A	Defence	Vigilance	Vigilance	Foraging	Fecundity
B	Courtship	Courtship	Defence	Nest Guarding	Parental Care
t_A	time invested in defence	time invested in vigilance	time invested in vigilance	time invested in foraging	energy invested in offspring production
b_A	probability of retaining territory	probability of surviving	probability of surviving	probability of surviving	reproductive success
b_B	probability of attracting a female	probability of attracting a female	probability of owning a territory	probability of offspring survival	survival of offspring
α	ability to defend	ability to detect and avoid predators	ability to detect and avoid predators	foraging efficiency	efficiency of investment in egg production
β	ability to court	ability to court	ability to defend a territory	ability to guard nest effectively	ability to care
γ	value of a territory without a female	value of surviving without breeding	value of surviving without a territory (i.e. as a floater)	value of surviving without successfully fledging young	survival of offspring when they are not cared for

General Results

A number of intuitive results immediately emerge from the model. Higher abilities when performing behaviour *A* lead to a decrease in the time spent doing so, relative to lower abilities (figure 6.1). Reduced investment in behaviour *A* at high abilities is seen for a wide range of parameter values. When performing behaviour *A* has a high impact on fitness in the absence of behaviour *B* (high γ), investing time in *A* becomes more important (figures 6.1 and 6.2). Additionally, when behaviour *A* is extremely valuable in the absence of behaviour *B*, individuals should invest all their time or energy in *A*, especially when their ability to do so is low ($\gamma = 0.8$, $\alpha < 2$, figure 6.1).

An interesting, counter-intuitive result emerges when the ability to performing behaviour *B* increases. One might expect individuals more able to perform behaviour *B* to invest less time in doing so, as shown for increasing α (figure 6.1). This is because individuals can gain the same benefits from reduced time investment if their ability to perform the behaviour is higher. Indeed, this is what occurs, but only when considering moderate (intermediate values of β) to high (approaching β_{max}) ability to perform behaviour *B* does an increase in ability lead to a decrease in time invested in *B* (figure 6.2). When the ability to perform *B* is low, any increase in ability (β) leads to an increase in the time spend engaged in behaviour *B*. Thus, optimal time or energy investment in *B* first increases and then decreases when the ability parameter (β) is increased. This pattern is robust to changes in both γ and α, and is more pronounced when *A* is valuable in the absence of *B* (high γ; figure 6.2a), and when ability to perform *A* is low (low α; figure 6.2b). Possible explanations for this effect are discussed below.

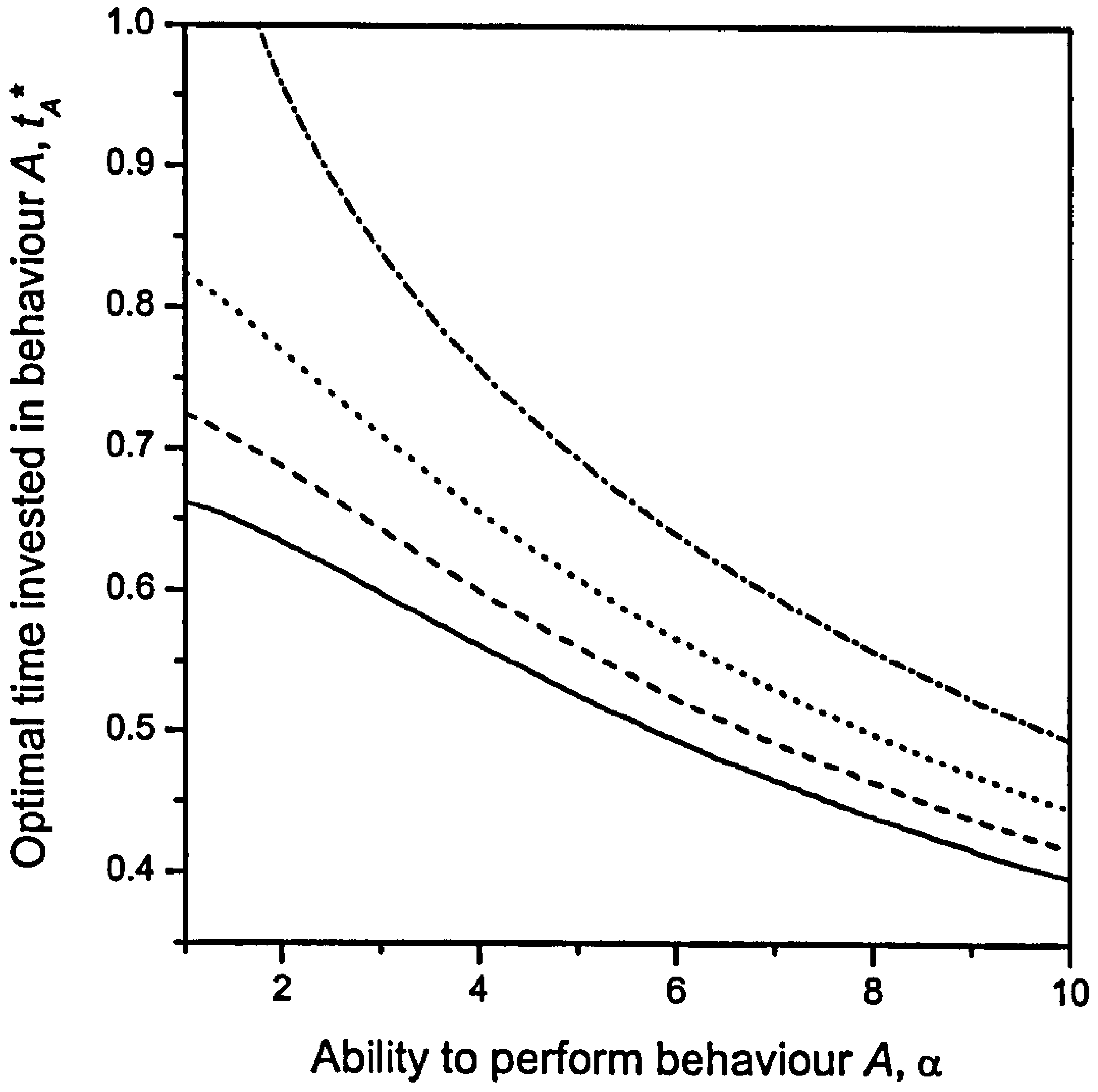


Figure 6.1: The effect of increasing the ability to perform behaviour A, α, on the optimal proportion of time or energy devoted to behaviour A, t_A*. Results are plotted for four values of γ, the value of performing behaviour A and not behaviour B. (γ = 0.2, solid line; γ = 0.4 dashed line; γ = 0.6, dotted line; γ = 0.8, dash-dot line). In all cases, $\beta = 5$, $\alpha_{max}=10$.

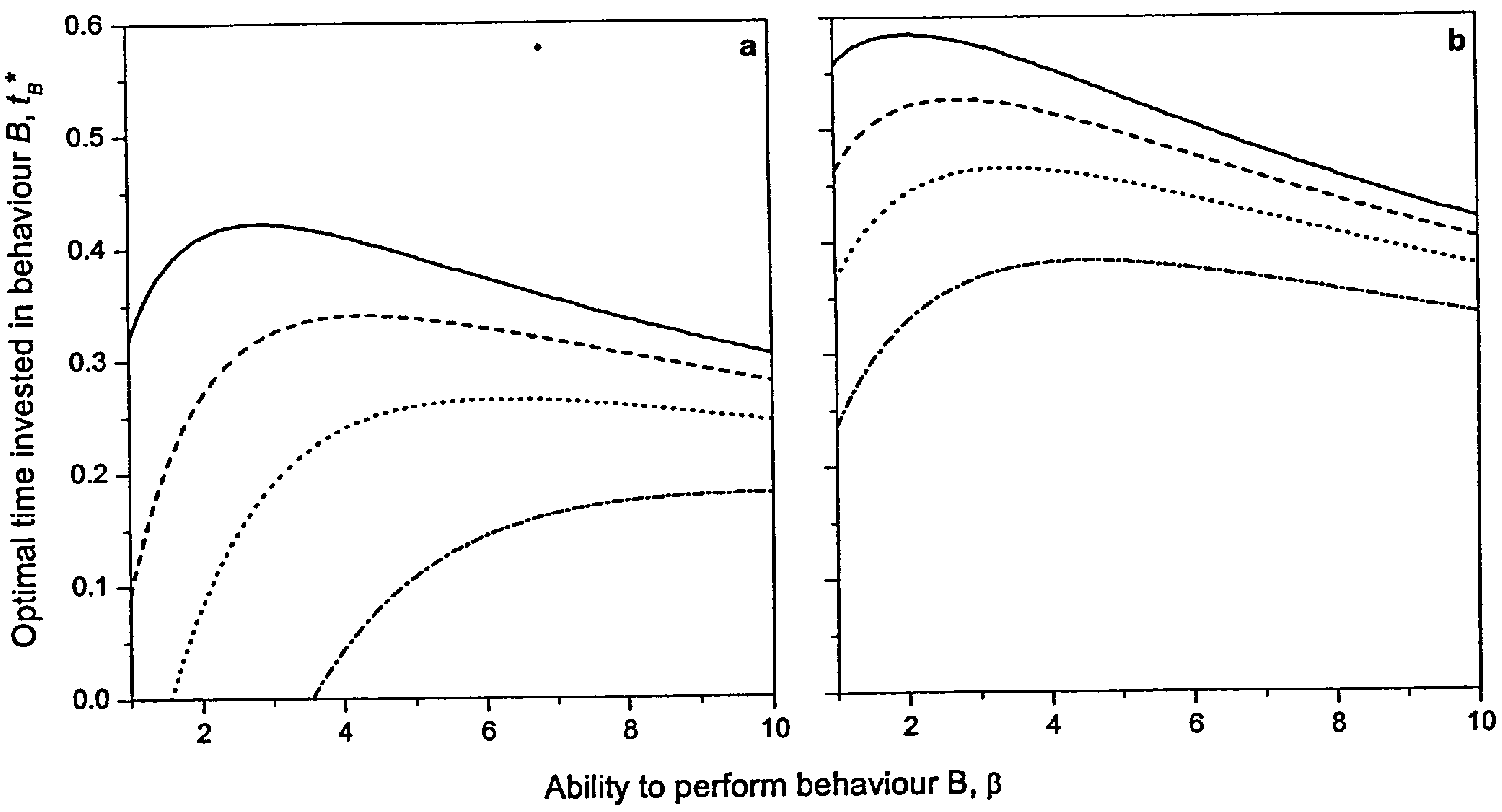


Figure 6.2: The effect of increasing the ability to perform behaviour B, β, on the optimal proportion of time or energy devoted to behaviour B, t_B*. (a) Individuals have lower ability to perform behaviour A, $\alpha = 3$, (b) Individuals have higher ability to perform behaviour A, $\alpha = 7$. Results are plotted for four values of γ, the value of performing behaviour A and not behaviour B. ($\gamma = 0.2$, solid line; $\gamma = 0.4$ dashed line; $\gamma = 0.6$, dotted line; $\gamma = 0.8$, dash-dot line). In all cases, β_{max}=10.

Discussion

Table 6.1 outlines several examples of pairs of behaviours that could be in conflict and thus form the basis of a trade-off in terms of time or energy. I will now discuss the findings and limitations of the model with reference to several of these examples. I discuss also the implications of the findings for the study of trade-offs between behaviours.

The patterns seen when the ability parameter α and the value of performing A in the absence of B (γ) increase are as intuition suggests. In the example of a trade-off between territory defence and female courtship discussed in the Introduction, this suggests that as a male becomes increasingly able to defend his territory (increasing α), the time he invests in doing so (t_A) decreases. In this example, γ describes the relative value of retaining a territory without attracting a female to breed on it. When territories hold high value without females, males invest more time in defending their territory, due to the survival benefits outside the breeding season. When territories are used solely for reproduction, more time is invested in courtship, although defence is still important since the territory must be retained in order to gain matings and raise offspring.

The parameter γ describes only the value of performing one behaviour in the absence of another, (in the above example, the relative values of territories with and without females present). Thus, territories (or foraging sites, etc.) are all assumed to be of equal intrinsic quality. In reality, territory quality is likely to vary amongst individuals, and this is likely to impact on the trade-off between defence and other behaviours. High quality territories may attract increased numbers of intruders (reviewed in Adams 2001), impacting on a male's ability to successfully defend his territory. Territoriality may also act as a surrogate for courtship, as females could obtain information on male quality by observing his defensive ability, reducing the need for additional courtship behaviour (e.g. Gronstol 1996). Females may also be attracted to high quality territories, allowing males to invest more in defence (Real 1991, Reynolds 1993), or females may be attracted to a mixture of both territory quality and male courtship (e.g. Uy et al. 2001; Candolin 2003). Additionally, these aspects may be correlated: a high quality male may possess a high quality territory (Heg et al. 2000), and males on high quality territories may show increased mating success (e.g. Trivers 1976; Howard 1978; Borgia 1979; Alatalo et al. 1986). Courtship rates may also be an indicator of territory quality (Itzkowitz and Haley 1999; Santangelo et al. 2002). Many factors may thus correlate with territory quality, and the causal relations are not always clear, as outlined above, and may indeed be species specific. The assumption that all territories are of equal intrinsic quality allows investigation of the parameters describing an individual's ability in the absence of the complications described above, and increases the generality of the model and its applicability to different behaviours.

The model assumes that behaviour A has value in the absence of B, but B has no value in the absence of A, and therefore never predicts that individuals should abandon A in favour of B, although B may be abandoned in favour of A. For example, if an individual were choosing between predator vigilance (A) and courting a potential mate (B), abandoning vigilance could result in death through predation, but abandoning courtship may allow the individual to survival to the next breeding season, where they would have a further opportunity to court mates, depending on the value of surviving without breeding (γ) in a particular breeding season (see table 6.1 for further examples). The model focuses on selecting optimal behaviour during the course of a single breeding season, and this behaviour may not be optimal if performed over the course of several seasons. For example, an individual that is constantly vigilant and does not breed in a season can gain positive fitness as it can potentially survive and reproduce next season. However, if it behaved in the same way in subsequent breeding seasons, it would never breed, and so would have no fitness. The value of surviving without breeding (γ) would therefore be effectively lower than if it had invested less in vigilance, and the consideration of multiple breeding seasons and the long term reproductive potential of individuals would be a valuable extension of this model.

It is possible that behaviour *B* could be of some value in the absence of behaviour *A*. For example, an individual investing nothing in territorial defence (and existing as a floater) may be able to reproduce by courting females already mated to territorial males, as they may potentially gain offspring as an extra-pair mate to the female (e.g. Dunn et al. 1994). Where behaviour *A* is fundamental to survival (for example, foraging or predator vigilance, see table 6.1), an individual investing only in behaviour *B* may be able to gain a little reproductive success before death. However, so long as this chance is small compared to the reproduction of individuals investing more in *A*, the results of the model are likely to remain valid.

The most interesting finding is that, under some conditions, increasing an individual's ability to perform behaviour *B*, β, can lead to an increase in the time spent performing *B*, rather than the decrease that one might expect. An explanation for this effect is that when individuals are less able to perform a behaviour, they gain greater benefits by investing little time in that behaviour and concentrating instead on performing the other behaviour. For example, if an individual must choose between predator vigilance and an aggressive behaviour such as territorial defence, and is of low fighting ability (for example, a younger or smaller animal), it would gain greater benefits from increased predator vigilance. As the individual becomes better able to fight (for example, older or larger), fights are more likely to be successful (Jennions & Backwell 1996, Beaugrand et al. 1996, Petersen & Hardy 1996, Johnsson et al. 1999), and so more time can be invested in aggression. As the individual's fighting ability increases further, its success in fighting or defence increases further (it could, for example, win a fight more quickly, as it is relatively larger than its opponent (e.g. Maynard Smith & Parker 1976, Enquist & Leimar 1983, Jennions & Backwell 1996, Hack 1997, but see Taylor & Elwood 2003) and consequently, less time needs to be invested in defensive behaviour.

When considering the trade-off between courtship and survival (scanning for predators), Houston et al. (2003) found a similar counter-intuitive pattern of optimal courtship with increasing male quality, where quality influenced male survival. In the current model, the ability parameters describe different aspects of quality. This allows for the possibility that a male which is highly ranked in one behaviour may not necessarily be highly ranked in another. For example, dominant males who are highly aggressive may not necessarily be the most attractive to females (Qvarnström & Forsgren 1998). The current model also assumes that one of the behaviours can only occur in the presence of the other; one of the behaviours is crucial (behaviour *A*) prior to the success of the other (behaviour *B*). Importantly, the counter-intuitive pattern is seen only when the ability of an individual to perform the less crucial of the behaviours (β) changes, otherwise, the changes are as intuition suggests.

The current model considers the optimal choices of a single individual. Incorporating the influence of other members of the population on the optimal time allocation decisions of an individual would be a potentially fruitful avenue of further research. For example, the courtship success of a male may depend not only on his own courtship effort but also on the courtship effort of his competitors (Reynolds 1993; Houston et al. 2003; Morrell & Kokko 2004, **chapter 7**). A game-theoretic treatment would be needed in such an extension of the current model.

WHAT DO THE FINDINGS MEAN?

Few, if any, published studies of behavioural trade-offs seem to have looked at how behaviours change with ability, and thus there is little empirical evidence for behaviours showing this pattern. This suggests that such trade-offs may need to be studied more closely, and variation in abilities considered, in order to understand fully how time invested in two different behaviours varies with the fitness trade-off associated with each behaviour under consideration.

The counter-intuitive resolution of the conflict between behaviours found in this and other studies (Houston et al. 2003) suggests that it may be difficult to determine whether or not a trade-off is occurring between two behaviours in empirical systems. An empirical investigation designed to seek a change in time allocation behaviour may find no change as a result of the response patterns predicted by models. For example, in a study of courtship and defence in the beaugregory damselfish, no differences were found in the time allocation to the two behaviours when territory quality was changed (Santangelo et al. 2002). The authors of that study suggested that territory quality may influence an individual's courtship and defensive behaviours. In terms of the current model, territory quality may have influenced the parameters α and β. Thus, if courtship ability (β) is affected by territory quality, the lack of an observed change in the time-allocation behaviour could be explained by the model's predictions.

The model may also apply to trade-offs involving energy rather than time. If limited energy is available to invest, an individual must decide how to allocate that energy, and its ability to invest is likely to affect that trade-off in the same way that the ability to perform a behaviour affects the time invested in that behaviour. For example, energy could be invested in either fecundity, or parental care, or a combination of both (Badyaev & Ghalambar 2001). Fecundity may be limited by body size (Reiss 1989), and parental care could be limited by the parents' ability to find food for the offspring (Whittingham & Robertson 1994, Turner & McCarty 1998). Studies investigating the trade-off between fecundity and parental care may mistakenly conclude that the trade-off is not affected by the parents' ability to care, as a result of the counter-intuitive patterns predicted by the model.

Although empirical studies investigating the effect of individual ability or quality on the trade-off between behaviours may find no apparent effect, awareness of a potentially counter-intuitive resolution of the conflict may be beneficial to understanding the trade-off. The current results suggest that further investigation may be warranted, to discover whether there is truly no effect, or a more subtle pattern is present. Closer examination of individual behaviour could reveal that ability to perform the behaviour alters under different experimental conditions. Beaugregory damselfish increase the rate at which they perform aggressive and courtship behaviours when on high quality territories (Santangelo et al. 2002). Territory quality may also affect ability to perform a behaviour if, for example, predation was higher on a low quality territory (Itzkowitz & Haley 1999), or territory quality is determined by food resources. Thus both the change in the external environment and the effect this may have on the individual should be considered.

Although it may be difficult in practice to alter the ability to perform one behaviour while leaving the ability to perform the other behaviour unmanipulated, and ability itself may be a difficult concept to measure, such work could provide valuable insight into trade-offs between behaviours. A potential method for this would be to manipulate the ability of individuals through learning (e.g. Brown & Laland 2003), endurance training (e.g. Kolok 1999; Plaut 2001), or prior experience (Hsu & Wolf 1999) such that groups of individuals trained to different levels can be compared. Additionally, external environmental factors (e.g. resource availability, territory quality) could be manipulated where these are known to affect the ability of individuals (Humphries et al. 1999; Santangelo et al. 2002; Houston et al. 2003). The model suggests that when factors influencing ability (e.g. territory quality) are manipulated, the use of two groups (i.e. high and low) may not reveal complete information regarding the trade-off between two behaviours. Instead, a number of groups encompassing a range of abilities should be considered to reveal whether counter-intuitive patterns exist in a particular study system. For example, if food availability or territory quality is known to influence ability, several different levels of availability or quality should be investigated.

Consideration of other factors that may affect individual quality or ability, such as predation risk, valuation of a disputed resource and motivation to perform a behaviour, may also be necessary. The complexity of behavioural trade-offs may make it difficult to tease apart the behaviours noted in natural systems, but this and other models (Houston et al. 2003) suggest one potential explanation for situations where the trade-off between two behaviours is not as predicted by verbal reasoning.

CHAPTER 7

HOW THE BOWERBIRD LOST ITS JEWELLERY: CAN TOO STRONG FEMALE CHOICE DETERIORATE MALE ORNAMENTATION?

Abstract

Competition for limited resources can have fundamental implications for population dynamics. However, the effects of resource depletion have rarely been discussed in the context of sexual selection, even though mate choice typically favours males who outperform others in securing access to some limited resource. Here, we develop a model to investigate the question of resource competition as a form of male-male competition in the context of male sexual displays. We phrase our model in terms of male bowerbirds either searching for or stealing resources (ornamental objects) valued by females, and compare the model findings to published studies of time allocation to various activities in different species of bowerbirds. The basic idea of the model, however, extends to cases where the resource is used less directly for the development of sexual ornamentation, such as males excluding others' access to food. We show that if males compete for resources used in sexual displays, intense female preference for high quality displays can lead to poorer prospects for efficient choice by females. This is because males benefit from excluding others' access to resources used in displays, damaging the overall efficiency of resource use in the population, and the accuracy with which females can judge male ability to gain such resources. The evolution of female choice may therefore have a self-limiting nature when it poses a selection pressure on male resource acquisition.

Introduction

Animals regularly find themselves in competition for limited resources, and such contests can have fundamental implications for population dynamics. When competing for a resource that takes effort to locate, animals have two choices: to search for it themselves or to steal the resource from others. For example, in the context of foraging, the decision to steal the resource from others leads to kleptoparasitism, which encompasses a range of behaviours, from the raiding of food hoards through to aggressively gaining access to a food resource (reviewed in Giraldeau & Caraco 2000). The term kleptoparasitism is technically used to refer to interspecific food stealing (Brockmann & Barnard 1979; Ha & Ha 2003), but the range of behaviours applies equally to intraspecific theft.

The question of whether individuals should invest in selfish kleptoparasitism or intraspecific theft versus unselfish searching for a food resource has been considered extensively in producer-scrounger games (e.g. Barnard & Sibly 1981; Vickery et al. 1991, Giraldeau & Beauchamp 1999; Giraldeau & Caraco 2000). In these games, individuals can either search for food (producers) or search for other individuals that have located food (scroungers) but cannot do both simultaneously (Barnard & Sibly 1981; Vickery et al. 1991). An increase in the frequency of scroungers in the population decreases the rate at which food can be discovered, and hence decreases the benefits that can be gained by an individual (Parker 1984). The benefits gained from the producer-scrounger game are thus frequency dependent, and high levels of interference through scrounging appear, in population terms, to be highly detrimental (see Krause & Ruxton 2002).

While such interference has been extensively studied in the context of foraging, the effects of kleptoparasitism have rarely been discussed in contexts of sexual selection. An interesting example is 'prostitution' in Adelie penguins, where males allow extra-pair females to steal nesting material if they gain extra-pair copulations (Hunter & Davis 1998). Obviously, such exchange of limited resources (in the case of penguins, stones used to build nests) is not beneficial to the overall productivity of the colony. Here, we investigate the broader question of producing versus scrounging in the context of male sexual displays. We shall show that if males compete for resources that are used in such displays, intense female preference for high-quality displays can — paradoxically — lead to poorer prospects for efficient choice. This is because when sexual competition is intense, males benefit from tactics that selfishly elevate their displays at the expense of others. When such behaviour spreads, resources available to generate high-quality displays become diminished.

We phrase our model in terms of male bowerbirds searching for resources (ornamental objects) valued by females. It should be noted, however, that the basic idea of the model extends to cases where the resource is used for ornament development less directly, such as males excluding others' access to food, or to cases where males compete to provide females with nuptial gifts. Males of 15 of the 19 species of bowerbird build more or less elaborate ornamental bowers (Marshall 1954; Cooper & Forshaw 1977; Chaffer 1984; Borgia 1986), which are decorated with coloured items from the surrounding habitat, such as feathers, fruits, flowers, bones, shells and manmade items (Marshall 1954; Cooper & Forshaw 1977; Chaffer 1984; Borgia 1985, 1986; Diamond 1987). Females use bower quality and the number of decorations present on the bower as indicators of male quality, and thus bower quality is an important determinant of mating success in bowerbirds (Borgia 1985; Borgia & Mueller 1992; Borgia 1995; Madden 2003; but see Lenz 1994). Bower owners can obtain decorations in two ways, similar to the producing and scrounging methods of foraging: they can search for new items (producer), or raid other males' bowers (scrounger). The fact that males steal decorations has long been known (Marshall 1954 and references therein). The large numbers of decorations present on bowers (e.g. Borgia 1986; Hunter & Dwyer 1997), however, indicates that searching plays a major role in determining the number of decorations on the bower, and therefore the mating success of the bower owner.

The dilemma faced by bowerbirds differs from producer-scrounger games. Not only are the benefits of producing (searching) or scrounging (raiding) frequency dependent, in the sense that the total number of items gathered depends on the behaviour of others (as items can be stolen by competitors), but the benefit gained from those items is also frequency dependent. Unlike scrounging in foraging games, the benefits gained by stealing are both direct and indirect. The direct benefit is an increase the quality of the stealer's own bower. However, since female bowerbirds select mates on the basis of the quality of the bower and its decorations (Borgia 1985; Borgia 1995; Uy et al. 2001), a given bower's power to attract females will depend on the quality of the bowers of other males in the area. Clearly, bowerbirds face a double temptation to raid other males' bowers, as raiding not only increases the quality of a males' bower, it also has the indirect benefit of decreasing the quality of his competitors' bowers, increasing his ability to attract mates and therefore gain offspring. However, if raiding becomes common, then a male needs to spend more time on his bower in order to protect it from theft. Both raiding and bower defence therefore conflict with time spent searching for new decorations. Additionally, a male must be present on his bower in order to mate with females, and this also therefore conflicts with the time spent searching for new items, but allows a male to defend the bower against intruders.

If the conflicts between the costs and benefits of raiding and remaining on the bower lead to a decrease in the time available for searching, this poses the question of why the bowerbird mating system does not collapse into selfish raiding and no searching. Here, we develop a game theory model to determine the evolutionary stable allocation of time to raiding, searching and remaining on the bower, and ask how this allocation influences the quality of the bower as a sexual ornament. Thus, we can investigate the impact of male-male competition for resources, and the influence of female choice on the quality of male sexual ornaments. We can imagine two potential scenarios: bower quality increases with the intensity of female choice as males strive to produce the best bower, or alternatively, bower quality declines when females become choosier, as males increasingly raid each others' bowers in order to maximise the difference between their bower and those of their opponents.

The Model

A male bower-owner's strategy consists of the way he divides his available time between three mutually exclusive activities: being in residence at the bower, *B*, searching the surrounding habitat for new decorations or other materials to improve the quality of his bower, *S*, and raiding the bowers of other males in order to steal decorations, *R* (see table 7.1 for parameters and definitions). Being in residence at the bower allows a male to tend and defend the bower and also allows him to observe the surrounding habitat for the presence of male intruders or females. The aim of the current model is to determine the evolutionarily stable proportion of time spent in these three activities (the evolutionarily stable strategy, ESS), where the strategy used by the population $\{B_p, S_p, R_p\}$ cannot be invaded by a more successful alternative mutant strategy $\{B_m, S_m, R_m\}$. Throughout, we use the subscripts p and m to refer to the population and the mutant respectively.

Table 7.1: Model parameters and definitions

Parameter	**Definition**
B	Time invested in tending the bower
S	Time invested in searching for decorations
R	Time invested in raiding other bowers
α	Efficiency of searching compared to tending
β	Efficiency of raiding compared to tending
γ	Female discrimination
δ	Deterioration of bower quality over time
Q	Quality of bower.
W	Fitness of mutant bower owner

Bower quality, Q, ranges from zero to one, where one refers to the highest possible quality bower and zero the lowest. Bower quality increases through three processes. Firstly, bower quality increases through tending the bower (for example, maintaining the bower walls or arranging newly acquired decorations), at a rate proportional to the time spent at the bower, B. Bower quality also increases when the owner searches for and finds new items or successfully raids other individuals' bowers. The rate of acquiring new items by either of these activities is denoted by A.

Total increase in bower quality depends multiplicatively on A and B, as both tending the existing bower decorations and bower structure and searching for new decorations are necessary to maintain quality (for example, newly acquired items will not improve the quality of the bower if the amount spent tending is zero). Furthermore, bower quality cannot increase indefinitely, because of structural constraints. We therefore assume that the best possible bower is indicated by its quality equalling 1, and any increase in bower quality is proportional to the scope for improvement of the bower, $(1 - Q)$. Bower quality therefore improves at a rate AB $(1-Q)$, which counteracts the natural decay through deterioration over time. This rate of natural deterioration is assumed constant, δ. Additionally, bowers decline in quality when they are raided, and we now proceed to specify these rates.

We assume that raiding is only successful when the owner of the bower being raided is not present on the bower $(1\text{-}B)$. If the owner is present, we assume that he can successfully defend his bower, which makes raiding attempts unsuccessful. We assume that males cannot predict whether an particular bower owner will be present when choosing to visit a bower. For example, bowers may be located such that a given male is unable to view his neighbours bowers. The benefits gained from raiding are also proportional to the quality of the bowers being raided, Q_p: it is impossible to gain any decorations from bowers that lack them in the first place. Thus, for the population, the bower quality gain from searching and raiding is:

$$A_p = [\alpha S_p + \beta R_p(1 - B_p)Q_p] \tag{1}$$

The loss of quality due to other males raiding the focal bower is similarly $-\beta R_p(1-B_p)Q_p$.

Here, α describes the efficiency of searching as a method of increasing bower quality in relation to tending the bower (that is, the increased amount by which bower quality can increase per unit time spent searching, compared to the potential increase from being present on the bower), and β describes the efficiency of raiding in relation to tending the bower. Thus, for $\beta = 3$, an individual will, all other factors being equal, gain three times as much bower quality through one time unit spent raiding compared to one time unit spent tending the bower. Of course, all other factors may not be equal, such as the quality of the bowers available for raiding (if large, this makes raiding relatively more rewarding); these are included in the equations as specified above.

For the mutant, the benefits of searching and raiding are described by:

$$A_m = [\alpha S_m + \beta R_m(1 - B_p)Q_p] \tag{2}$$

We can now proceed to specify the equilibrium conditions for bower quality. For the population, the change in bower quality over time is:

$$dQ_p \Big/ dt = A_p B_p (1 - Q_p) - \left[\delta + \beta R_p (1 - B_p) Q_p\right] \qquad (3)$$

Solving for d*Qp*/d*t* = 0, we obtain the equilibrium bower quality in the population:

$$Q_p = \frac{1}{2\beta(B_p - 1)B_p R_p}\left(\delta + \beta(B_p - 1)^2 R_p + \alpha B_p S_p - \sqrt{D}\right) \qquad (4)$$

where

$$D = -4\alpha\beta(B_p - 1){B_p}^2 R_p S_p + (\delta + \beta(B_p - 1)^2 R_p + \alpha B_p {S_p}^2) \qquad (5)$$

For the mutant, changes in bower quality are described analogously to equation 3:

$$dQ_m \Big/ dt = A_m B_m (1 - Q_m) - \left[\delta + \beta R_m (1 - B_p) Q_p\right] \qquad (6)$$

And the equilibrium bower quality for a mutant in a population using strategy {B_m, S_m, R_m} is:

$$Q_m = -\frac{B_m(\beta(B_p - 1)Q_p R_m - \alpha S_m)}{\delta + \beta(B_m Q_p R_m - B_m B_p Q_p R_m + R_p - B_m R_p) + \alpha B_m S_m} \qquad (7)$$

We still need to make assumptions about the benefits of having a bower of specific quality. In bowerbirds, females choose males to mate with following assessment of the quality of several bowers (Uy et al. 2000, 2001). Thus, fitness of a bower owner depends on the quality of the bower relative to other bowers in the population. However, species or populations might vary in the choosiness of females. If females are very choosy, they will presumably mate with the owner of the best bower even if the male is not available at the bower much of the time, whereas if mating is random, 'passive attraction' (sensu Parker 1983) to males who are available will determine mating success. These effects can be incorporated in a single equation if we assume the following fitness for the mutant bower owner, *W*:

$$W = B_m \left(\frac{Q_m}{Q_p} \right)^{\gamma} \tag{8}$$

Here, γ describes how discriminating females are. If γ is high, females pay a great deal of attention to bower quality, mating only with males who have good quality bowers relative to the rest of the population; females are thus extremely choosy. If γ is zero, females pay no attention to bower quality, and mate randomly with any male who is present on his bower.

In order to find the optimal allocation in three different tasks $\{B, S, R\}$, we perform a numerical search. Beginning with a randomly selected population strategy, we test all mutant strategies where one of the components (*B*, *S* or *R*) is increased or decreased by 1% compared to the population strategy. The resulting strategy is then normalised so that $B+S+R = 1$. The mutant strategy giving the highest fitness becomes the population strategy for the next generation. We iterate for 2000 generations until an ESS is reached. The above procedure only yields one ESS at a time; however, starting from different randomly chosen values for the population strategy, we never found a case of alternative ESSs.

Results

We investigate the effect of varying the efficiency of searching (α) and raiding (β), the natural rate of deterioration of bowers (δ) and the degree to which females discriminate between bowers of different qualities (γ). This allows us to ask, for example, how much time males should devote to searching and raiding as opposed to remaining on the bower, waiting for females and carrying out bower maintenance activities, when raiding can be an ESS, and whether males should ever abandon the creation of bowers. We can also investigate how the quality of bowers can vary with these parameters.

Firstly, as the efficiency of searching for new items, α, increases, the ESS time spent searching for new items decreases slightly, whereas bower quality increases (figure 7.1a). This increase is more pronounced when bowers deteriorate more quickly ($\delta = 0.5$, figure 7.1b). As the time spent searching decreases, there is a corresponding increase in the time spent on or near the bower. Unsurprisingly, increasing the efficiency of raiding (β) leads to an increase in the time invested in raiding, and a corresponding decrease in the time spent searching (figure 7.2). Raiding, however, is not beneficial to bower quality in the population. As raiding increases in efficiency and therefore frequency, bower quality declines. At high values of raiding efficiency, bowers are of extremely low quality.

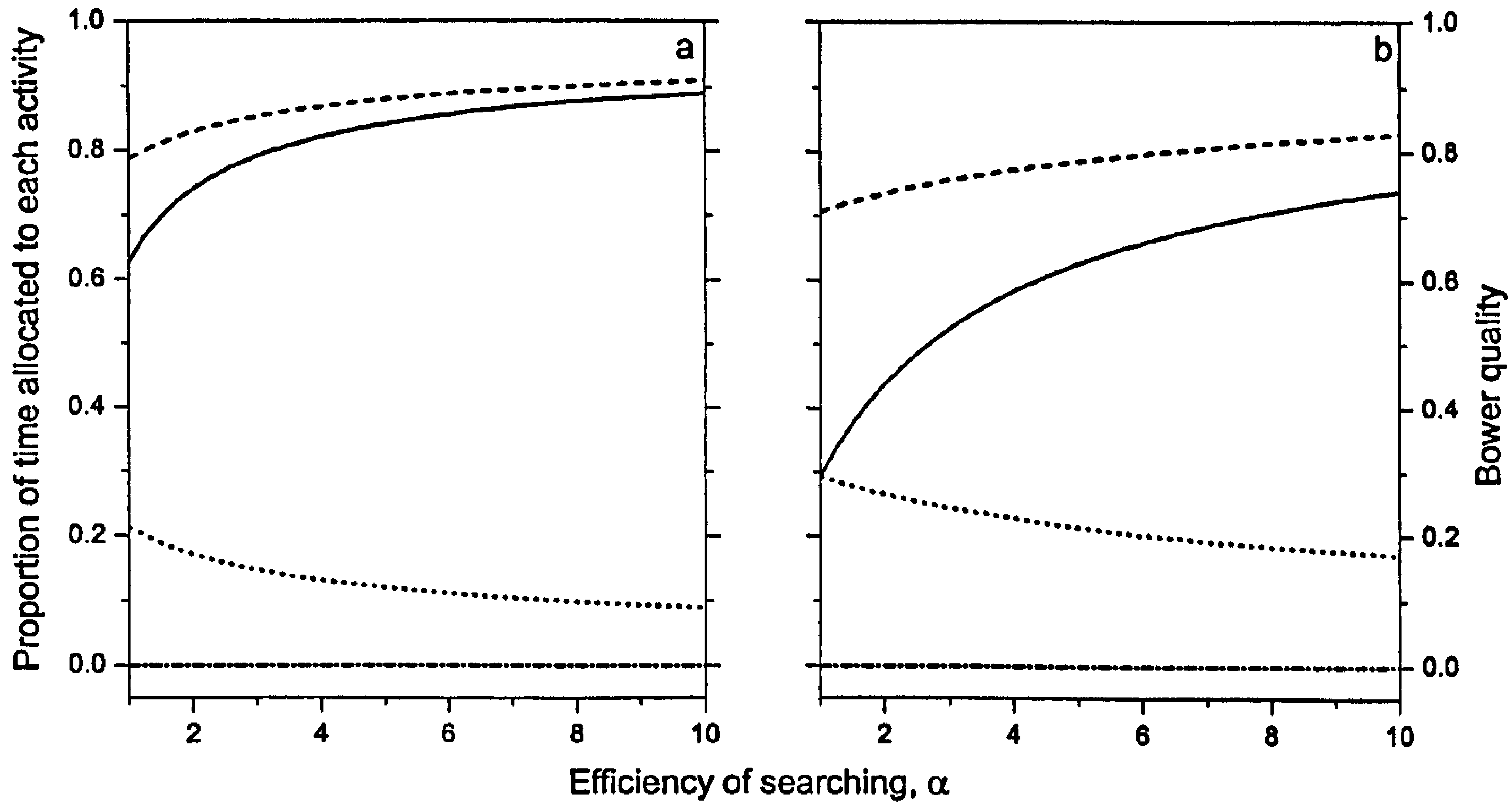


Figure 7.1: The effects of increasing the efficiency of searching (α) on the ESS probabilities of a male remaining on his own bower (B, dashed line), searching (S, dotted line) and raiding (R, dash-dot line), and the ESS quality of bowers in the population (Q, solid line), for two rates of bower deterioration (δ): a) $\delta = 0.1$ b) $\delta = 0.5$. Other parameter values used: $\beta = 1, \gamma = 1$

In many cases (figure 7.1) raiding is absent from the population. For raiding to occur, it needs to be a much more efficient way to obtain ornate objects than searching, but even when raiding efficiency greatly exceeds that of searching (figure 7.2), it still occurs very infrequently. Males spend less than 6% of their time raiding even when it is 100 times more effective as a method of improving bower quality than searching and tending the bower (figure 7.2, $\alpha = 1$). Potential explanations for the scarcity of raiding are considered in the discussion.

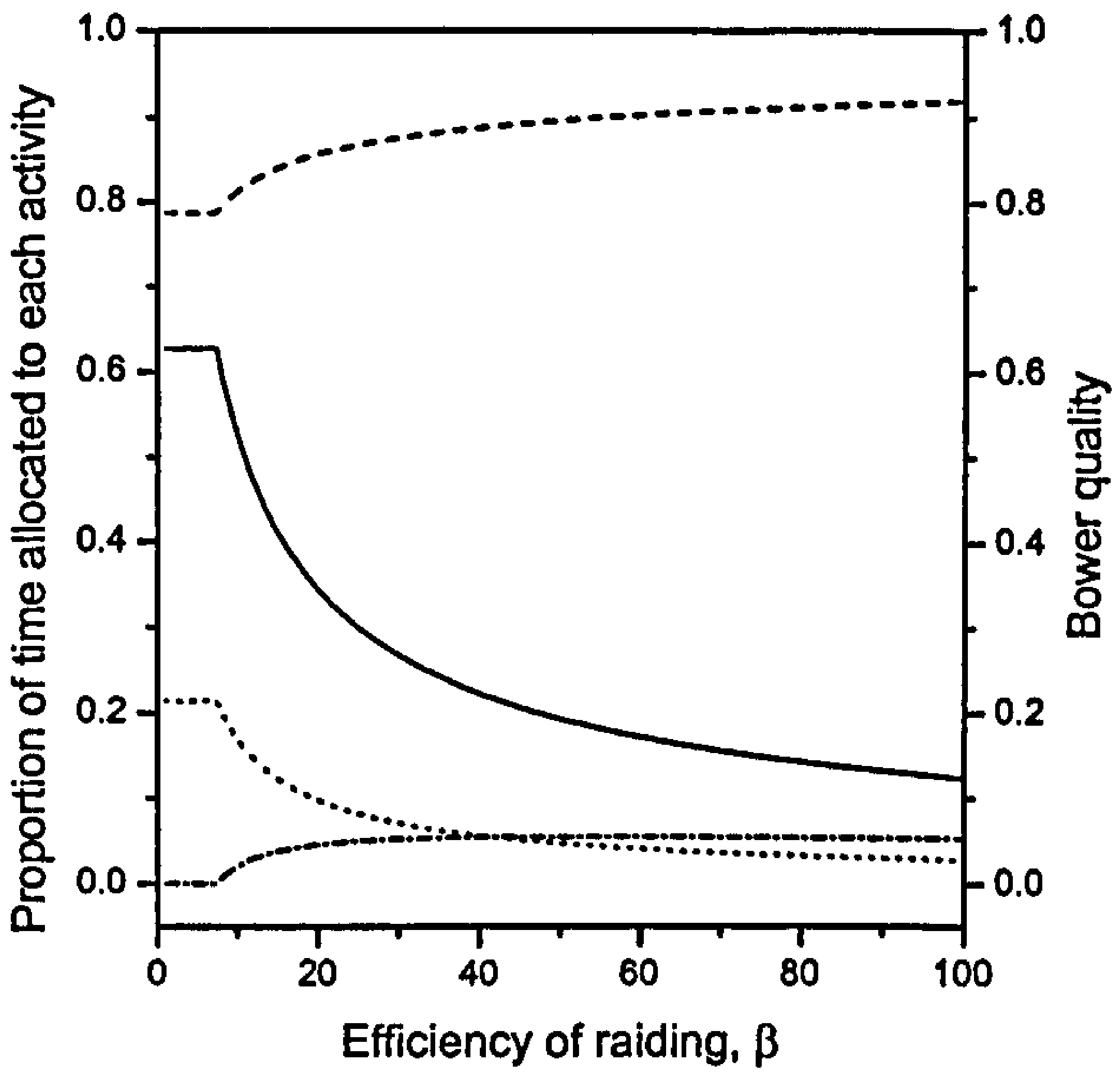


Figure 7.2: The effects of increasing the efficiency of raiding (β) the bowers of other males on the ESS probabilities of a male remaining on his own bower (*B*, dashed line), searching (*S*, dotted line) and raiding (*R*, dash-dot line), and the ESS quality of bowers in the population (*Q*, solid line). Other parameters used: $\alpha = 1$, $\gamma = 1$, $\delta = 0.1$.

When bowers naturally deteriorate more rapidly, males spend increased time searching for new decorations. Raiding, however, does not become more common in the population with increasing deterioration. Instead, males in a population without raiding (figure 7.3a) invest more time in searching in this case. Males in a population where raiding occurs (figure 7.3b) maintain approximately the same level of raiding regardless of the rate of deterioration, again, searching increases. Thus, male behaviour can compensate for changes in the external environment. As deterioration increases further, bower quality decreases (figure 7.3a), as the decline in bower quality through deterioration is not offset by the increased time spent searching.

When raiding occurs in the population (figure 7.3b), bower quality is low regardless of the rate of deterioration. These results also indicate that male behaviour (searching versus raiding) is a more important determinant of bower quality than the external rate of deterioration, and highlights the importance of studying male-male interactions.

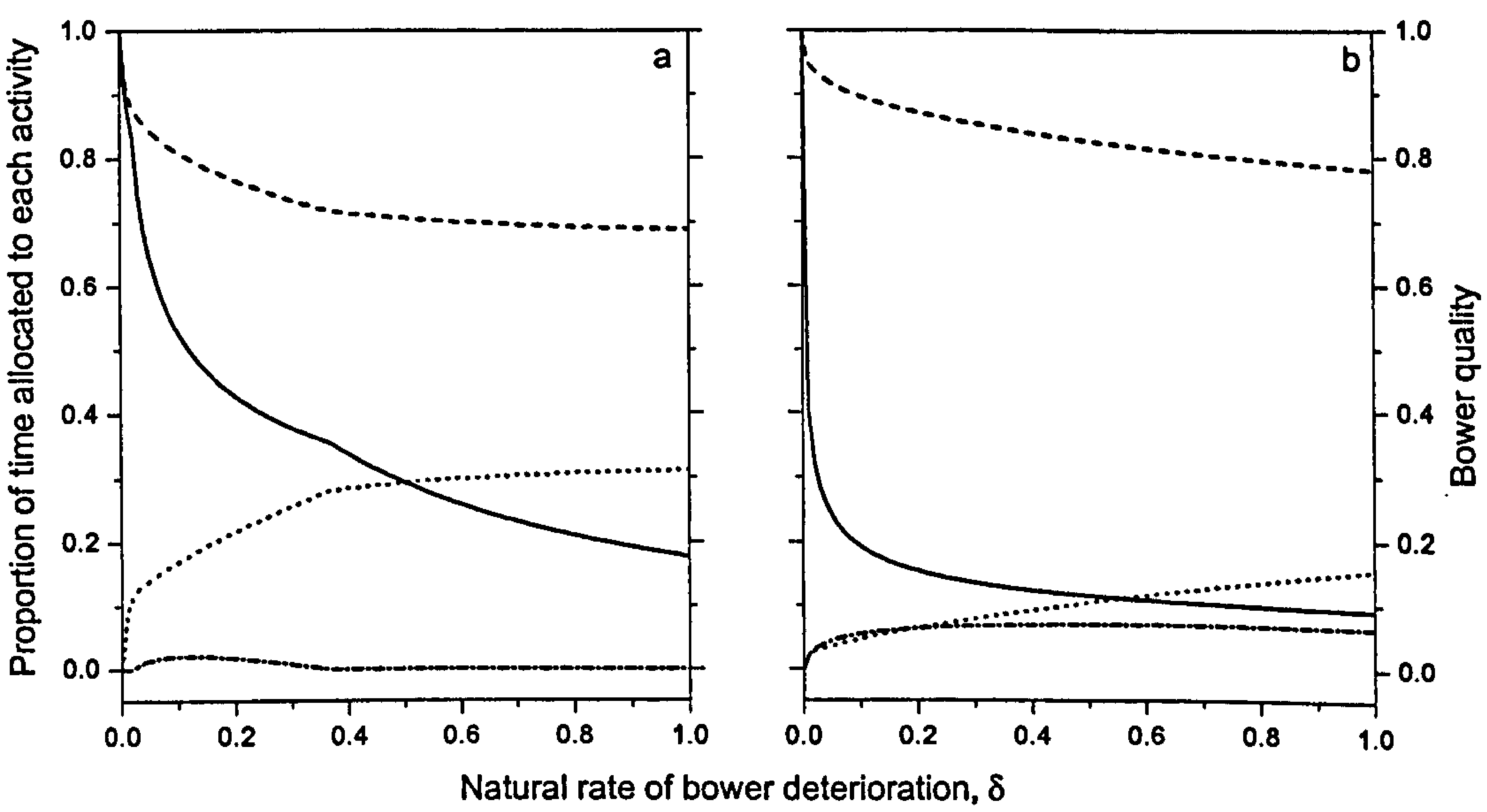


Figure 7.3: The effects of increasing the rate of natural bower deterioration (δ) on the ESS probabilities of a male remaining on his own bower (*B*, dashed line), searching (*S*, dotted line) and raiding (*R*, dash-dot line), and the ESS quality of bowers in the population (*Q*, solid line), for two different raiding efficiencies (β): a) β = 10, b) β = 50. Other parameters used: α = 1, γ = 1.

Finally, and most interestingly, we investigated the effect of female discrimination on male time investment and bower qualities. When females mate indiscriminately with whichever male is present on his bower (figure 7.4), males should spend all their time waiting at the bower and no time searching or raiding. In this case, bower quality is zero and males should abandon bower building altogether. As females become increasingly discriminatory, males spend more time searching for new items and less time waiting on the bower. Bower quality rises sharply even with low levels of female discrimination, and then declines, as females become even more discriminating (figure 7.4). This is an important and counterintuitive result: increasing female discrimination can lead to a decline in bower quality.

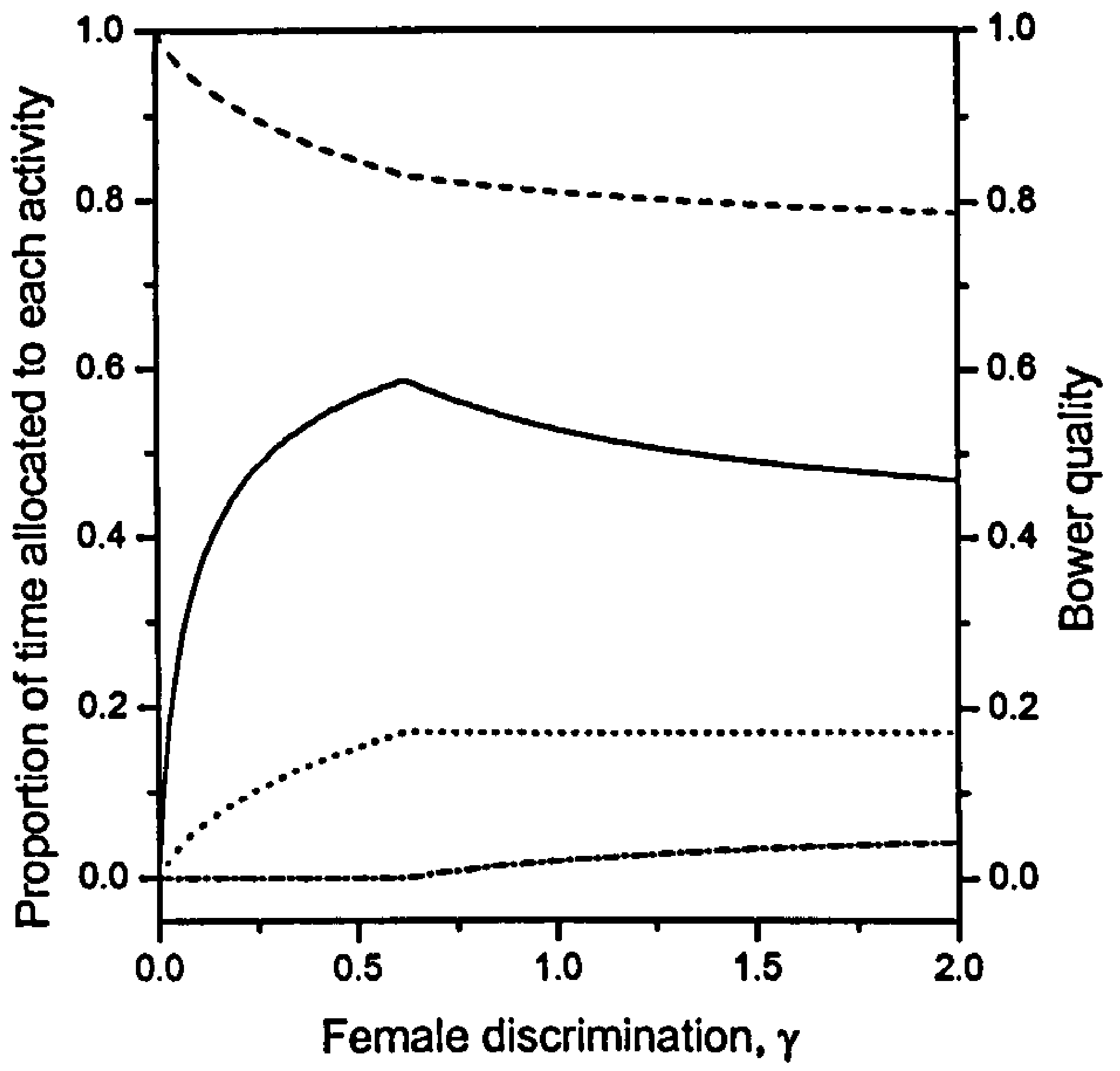


Figure 7.4: The effects of increasing discrimination by females are (γ) on the ESS probabilities of a male remaining on his own bower (B, dashed line), searching (S, dotted line) and raiding (R, dash-dot line), and the ESS quality of bowers in the population (Q, solid line). Other parameters used: $\alpha = 1$, $\beta = 10$, $\delta = 0.1$.

Discussion

Two main results emerge: Firstly, our model makes a number of predictions regarding time allocation in bowerbirds, and we compare these predictions with published results from a number of bowerbird species. Secondly, we discuss the predictions regarding the impact of female choice on male-male competition, and the potential effect of this competition on male ornamentation.

THEFT AND BOWERBIRD TIME BUDGETS

Our model predicts that breeding males should spend a large proportion of their time at the bower (around 70% or more, figures 7.1-7.3). However, observations of bowerbird populations, indicate substantial variation in the time spent at the bower, ranging from 3 to 73% (table 7.2). Our prediction is high due to our assumption that males must be present at the bower in order to protect their bower from raids and to find females (we assumed that females ignore bowers with no male present). Deviations from these assumptions may explain some of the discrepancy. The time spent at the bower may relate to the risk of being raided, as it does in our model: when raiding is more common, bower residence is predicted to be higher (figure 7.2). Although a 'common occurrence' (Lenz 1994; Pruett-Jones & Pruett-Jones 1994), raiding does not occur frequently in bowerbirds; studies suggest that a given bower is raided once every 4 days or less (Lenz 1994; Borgia & Gore 1986; Borgia & Mueller 1992; see table 7.2), or males spend only a small proportion of time engaged in raiding activities (Frith & Frith 1994).

Table 7.2: Presence on the bower and occurrence of raiding for a range of bowerbird species.

Species	**Mean % time at or near bower (range)**	**definition of 'near bower' where specified**	**Occurrence of theft**	**Source**
Satin Bowerbird *Ptilonorhynchus violaceus*	73	50m	0.11 thefts bower^{-1} day^{-1}	Donaghey 1981; Borgia & Gore 1986
Tooth-billed Bowerbird *Ailuroedus destirostris*	64 (52-79)	'attending court'	0.18 % of time	Frith & Frith 1994; Frith et al. 1994
MacGregor's Bowerbird *Amblyornis macgregoriae*	54 (20-75)	20m	No raiding occurs, but spend 2% of time interacting with intruders	Pruett-Jones & Pruett-Jones 1982, 1985
Great Bowerbird *Chlamydera nuchalis*	47.2			Veselovsky 1978
Spotted Bowerbird *Chlamydera maculata*	9.6 (8.8 – 10.4)	'at bower'	0.048 thefts bower^{-1} day^{-1}	Borgia & Mueller 1992; Madden 2002
Regent Bowerbird *Sericulus chrysocephalus*	3		0.264 thefts bower^{-1} day^{-1}	Lenz 1994

The assumption regarding female behaviour may explain the remaining discrepancies. Of the three species with comparable measures of raiding, Regent bowerbirds *Sericulus chrysocephalus* suffer the highest rate of theft, yet spent the least amount of time on the bower (table 7.2). However, this species differs from others in that courtship begins in the forest canopy rather than on the bower (Lenz 1994), and so the assumptions of our model are not applicable here. Spotted bowerbirds spend less time on the bower than satin bowerbirds, yet suffer a lower rate of theft (table 7.2), suggesting satin bowerbirds spend increased time on the bower to counteract the risk of raiding. However, to fully test this hypothesis, studies investigating both the risk of being raided and the time spent on the bower, both within and between species are needed. Our model is not restricted to bowerbirds: Penduline tits (*Remiz pendulinus*) face a similar time allocation problem. Males build nests to attract females, and theft of nesting material is more efficient than searching for it, reducing the time taken to build a nest. In this species, males spend up to 80% of their time near their nest, although much less time is needed for construction (Schleicher et al. 1993).

In our model, the damage caused by raiding is equal to the benefits gained by the raider, and at equilibrium, all males raid and are raided equally often. Such reciprocal raiding has been noted in bowerbirds (Borgia & Gore 1986; Frith et al. 1994). Raiding is often combined with bower marauding, where intruding males partially destroy an opponents bower in addition to stealing decorations (Pruett-Jones & Pruett-Jones 1994). Thus, the impact of raiding on the victim may exceed the direct benefits gained by the raider (decorations gained), suggesting that the intensity of raiding may be important. Modelling suggests that raiding may only be evolutionarily stable when combined with marauding (Pruett-Jones & Pruett-Jones 1994). At well-decorated bowers, however, males focus on stealing rather than marauding (Borgia & Gore 1986; Borgia 1995), thus, bower quality can impact on stealing behaviour (Madden 2002).

GENERAL LESSONS: MALE-MALE COMPETITION FOR RESOURCES AND SEXUAL SELECTION

A common feature of all sexual selection models so far is that female preferences cause the evolution, and sometimes exaggeration, of male traits (e.g. Lande 1981; Iwasa & Pomiankowski 1991; Pomiankowski et al. 1991; Kokko et al. 2002). To our knowledge, it has not been realised before that the effects of competition between males to attract mates can drive selection in the opposite direction. Our model suggests that intensely expressed preferences of females can cause the deterioration of male ornamentation through male-male competition (figure 7.4). In the context of the bowerbird mating system, this happens if raiding becomes more frequent as females become increasingly choosy. In a wider context, such an effect could occur whenever contests between males to acquire resources necessary for sexual displays lead to deterioration of this resource, in other words, reduced ability to invest in sexual ornaments forming the basis of female choice.

Further work is required to explore the consequences of this mechanism for the evolution of female choice. Could the diminishing male display also mean less accurate female choice, which would probably hamper the further evolution of female choice? This requires us to assess how accurately females distinguish between bowers of varying quality. In our model, at equilibrium, all bowers are of equal quality. However, in natural populations, variation will exist around any trait under consideration (Pomiankowski & Møller 1995). If we expect traits to vary around an equilibrium, the accuracy of female choice will depend on mean trait size as well as the variation available for assessment. Our results have established the self-limiting nature of female choice, whenever choice is easier when the mean male trait is larger. In other words, if strongly choosy females cause such intense male-male competition that traits evolve to be smaller, and if trait size is easier to assess when it is large, then choosiness leads to diminished prospects for accurate choice, and the benefits of being choosy become limited.

Under what conditions would we expect choice to be easier when traits are large or well developed? When a trait is on average large, it may be possible to have a larger variance around it, and thus discrimination may be easier for females. Whether this phenomenon occurs is a matter of empirical research rather than modelling, and thus we have not included it in our study, instead, we discuss here the prospects of finding such a mechanism in nature.

Sexually selected traits are often described as 'elaborate', suggesting that in general, they appear larger or more ornate when compared to other traits that do not form the basis of sexual selection. Darwin (1871) noted that sexually selected characteristics are highly variable, and suggested that this was to allow discrimination by potential mates. Recent meta-analyses (Alatalo et al. 1988b; Cuervo & Møller 1999; Cuervo & Møller 2001) have found a larger coefficient of variation in sexually selected traits than in ordinary morphological, naturally selected traits. A greater variance suggests that female choice for better quality males should be easier. However, there is little data at present regarding the accuracy of female assessment relative to the degree of trait exaggeration. We simply note here that it is plausible that larger traits have absolutely larger variances. It appears there is limited data on animals' ability to discriminate between traits of various sizes. Cognitive limitations have mainly been discussed in the context of detecting small degrees of asymmetries in sexual traits (Swaddle 1999a, b). In that context, animals appear unable to detect too small (within-individual) differences in the sizes of morphological traits. It is conceivable that a similar cognitive constraint operates when attempting to detect differences between different males; further work is needed in this area. Generally, signals are easier to detect with increasing difference between the signal and the background (e.g. Bushnell et al. 2003), but a minimum change in a signal is necessary before the change can be detected (Weber's law; e.g. Shettleworth 1998).

Whether choice really becomes self-limiting depends on how the mean and variance of male traits respond to male-male competition. Our model suggests male-male competition may hamper female choice. Alternatively, male-male competition may increase the variance in male sexual ornaments due to inequalities in resource use, or the abilities of lower quality males to tolerate the stress of competition. Such a pattern has been found in sticklebacks (*Gasterosteus aculeatus*), where competition between males enhances variation in coloration, used in female choice (Bakker 1994; Rowland 1994). Future models could incorporate variation in male quality (in terms of his ability to construct a high quality bower) and stochasticity in the males' decision making processes and success in developing an ornament and/or attracting females (McNamara et al. 1997).

Thus, while we have shown that there is a possibility for self-limiting evolution of female choice via deteriorating resource use efficiency under intense male-male competition, the details of the system may matter. Nevertheless, we have shown that too intense male-male competition can, at least under certain circumstances, lead to smaller ornaments and thus deteriorating accuracy of female choice. This could provide a natural stopping point for runaway evolution of male traits, something that open-ended models of runaway sexual selection require to be realistic (Kokko et al. 2003). To discover if such self-limitation occurs in nature, resource use and interference of males should be studied at different intensities of female choice, and we hope that our study encourages empiricists to do so.

CHAPTER 8

MATE GUARDING, MALE ATTRACTIVENESS AND PATERNITY UNDER SOCIAL MONOGAMY

Abstract

Socially monogamous species vary widely in the frequency of extra-pair offspring, but this is usually discussed assuming that females are free to express mate choice. Using game theory modelling, we investigate the evolution of male mate guarding, and the relationship between paternity and mate guarding intensity. We show that the relationship between evolutionarily stable mate guarding behaviour and the risk of cuckoldry can be complicated and non-linear. Because male fitness accumulates both through paternity at his own nest and through his paternity elsewhere, males evolve to guard little either if females are very faithful, or if they are very unfaithful. Attractive males are usually expected to guard less than unattractive males, but within-pair paternity may correlate either positively or negatively with the number of extra-pair offspring fertilized by a male. Negative correlations, whereby attractive males are cuckolded more, become more likely if variation in male attractiveness is high, if the reason behind female extra-pair behaviour applies to most females (e.g. fertility insurance) rather than the subset mated to unattractive males (e.g. when females seek 'good genes'), and if mate guarding is efficient in controlling female behaviour. We discuss the current state of empirical knowledge with respect to these findings.

Introduction

Females of numerous socially monogamous species, particularly birds, have been shown to actively seek extra-pair fertilizations (Westneat et al. 1990; Petrie et al. 1998; Griffith et al. 2002). For a female, having offspring fathered by a male other than her social partner has a number of potential benefits (reviewed in Jennions & Petrie 2000). These include improving the genetic quality of offspring (e.g. Hasselquist et al. 1996), genetic compatibility (Johnsen et al. 2000), security against infertility of her mate (Sheldon 1994; Krokene et al. 1998; Whitekiller et al. 2000), and inbreeding avoidance (Blomqvist et al. 2002; Foerster et al. 2003). Species vary widely in the frequency of extra-pair young: in birds, the observed frequencies range from 0 to 76% (Griffith et al. 2002; Westneat & Stewart 2003). Such variation has been explained by factors such as population density (Møller & Birkhead 1993; but see Westneat & Sherman 1997; Wink & Dyrcz 1999), breeding synchrony (Stutchbury & Morton 1995; but see Griffith et al. 2002), the magnitude of variation in fitness-related traits in the population (Møller 1997; Petrie et al. 1998), and the relative importance of male parental care (Møller 2000), amongst others (reviewed in Griffith et al. 2002).

The extensive review of extra-pair paternity by Griffith et al. (2002) does not mention mate guarding as a factor influencing paternity. However, if females are mating outside the pair bond, a male should endeavour to protect his paternity and guard against cuckoldry. While female infidelity can obviously select for mate-guarding behaviour (van Rhijn 1991; Fishman et al. 2003), it also implies that males can have fitness opportunities away from their own social mate, which could potentially select for males who maintain less physical proximity to their social mate. Whenever mate guarding plays a role in the sexual conflict over paternity, one should investigate how it influences the evolution of within- versus extra-pair paternity, and to what extent it limits the expression of female preferences (Green et al. 2002; Valera et al. 2003).

The matter is further complicated by plastic male and female behaviours. Females or males may follow adaptive rules of differential allocation where their reproductive effort and mating effort depend on the attractiveness, or quality, of their mate and themselves (reviewed in Magrath & Komdeur 2003; Sheldon 2000). It is reasonable to expect that optimal levels of mate guarding can be similarly plastic (Komdeur 2001). But should an attractive male guard more or less than an unattractive male, and should we consequently expect a positive or negative correlation between the paternity a male gains at home and elsewhere? Here we shall show, using game theoretic modelling, that the answer is not straightforward.

Both theoretically and empirically, mate guarding has been studied much more extensively in crustaceans and in insects than in vertebrates (e.g. Parker 1974b; Grafen & Ridley 1983; Carroll 1993; Jablonski & Vepsäläinen 1995; Jivoff & Hines 1998; Jormalainen 1998; Mathews 2002; Plaistow et al. 2003; Härdling et al. 2004). In non-vertebrates, pre- or postcopulatory guarding is maintained by continuous physical contact. In mate-guarding vertebrates (e.g. birds, lizards and primates), males cannot guard their social mates in this way. Instead, mate-guarding males maintain proximity to their females, and are thus at least partially able to fend off intruders or to form a disincentive for the female to seek potential extra-pair males. Male birds commonly accompany females almost continuously from before the onset of incubation. The guarding period thus coincides with female fertility. By guarding in such a way, males face a trade-off, as they cannot simultaneously maximise both within- and extra-pair paternity (Hasselquist & Bensch 1991). However, a compromise strategy, where males guard during the fertile period of their female and seek extra-pair copulations outside this time appears to be an evolutionary stable strategy (Fishman et al. 2003; see also Saino et al. 1999) when female fertility is asynchronous within a population.

However, there are many cases where males are unable to simultaneously achieve high success at home and elsewhere. In many species there is considerable overlap between the fertile periods of females, due to more or less synchronous breeding (Birkhead & Biggins 1987). Females may also store sperm to some extent (Birkhead 1998), which further extends the overlap between 'profitable' times to approach different females. In such cases, we may expect that males face a trade-off with respect to time. When a temporal separation of guarding and extra-pair activities is not possible, males must decide how much time to allocate to the two mutually exclusive activities of mate guarding and spending mating effort outside the pair bond. Currently we lack theory on how this conflict should be resolved, with two notable exceptions. Van Rhijn (1991) provided a simple simulation that highlights the frequency-dependent nature of the problem but does not solve for evolutionary equilibria, and Alonzo and Warner (2000) studied a specific system where mate guarding trades off with sperm production in a fish. Here, our aim is to develop general predictions on mate guarding and patterns of parentage in socially monogamous species.

The model

In our model, we assume that mate guarding can only be 100% efficient when it occurs 100% of the time (Chuang-Dobbs et al. 2001 and references therein; see also Johnsen et al. 1998), and that there is a trade-off between mate guarding and gaining extra-pair offspring (Gil et al. 1999; Hasselquist & Bensch 1991; but see Stutchbury 1998).

We assume that females' fertile periods are synchronous, and model the trade-off between mate guarding and mate acquisition by assuming that the male can only be performing one of these activities at a time. Thus, mate guarding is modelled as the time t (0 t 1) that the male spends 'at home' (i.e. in close proximity to his social mate). The remaining time $1-t$ is spent 'elsewhere' (away from the male's social mate), and during this time the male is free to search for extra-pair matings. For limitations of this assumption, see the Discussion. We assume that males can be either attractive or unattractive, and guarding time can vary according to attractiveness.

To predict male fitness, we must assume a function that relates a male's guarding effort and attractiveness to his paternity at home (within-pair paternity p_W), and elsewhere (extra-pair paternity p_E). Biologically reasonable functions for p_W and p_E must satisfy the following conditions:

1. Within-pair paternity p_W should obtain values between 0 and 1. It should be an increasing function of t, the male's own guarding effort, and of t_{pop}, the mean guarding time used by males in the population. The latter relationship

arises because guarding males will not be able to attempt cuckoldry as often as non-guarding males.

2. Extra-pair paternity p_E should decrease with t and with t_{pop}, for similar reasons as above.
3. If males vary in attractiveness, more attractive males should achieve more within-pair paternity than less attractive males, for the same guarding effort. Likewise, they should achieve more extra-pair paternity, if the time spent not guarding is the same. With diminishing differences in attractiveness and guarding time between males, the expected paternities achieved should approach each other as well.
4. The distribution of paternity in the whole population must satisfy self-consistency (Queller 1997; Houston & McNamara 2002; Kokko & Jennions 2003). This means that the total paternity achieved by all males must sum up to 1 per brood; for example, it is impossible that all males achieve 100% within-pair paternity and also gain paternity in other broods.

A very large number of functions relating guarding time to p_W and p_E exist that satisfy the above criteria, and it is not feasible to study every possibility. We chose to study two very different, and flexible, families of functions for p_W. We examined the following two possibilities:

$$p_W(t,k) = \frac{t}{t + k(1-t)^g c_{pop}} \qquad (1a)$$

and

$$p_W(t,k) = g\, t^{kc_{pop}} \qquad (1b)$$

In these equations, the parameter k measures female infidelity. This is a measure of the eagerness with which females, paired to a male of specific attractiveness, seek extra-pair copulations (and consequently how good they are at escaping male mate-guarding efforts). k will have different values for different males, if these differ in attractiveness. In our examples, we have either assumed no variation (same k for all males), or that a proportion x of males are highly attractive and experience female infidelity k_1, and the remaining $1-x$ are less attractive and experience infidelity $k_2 > k_1$. The infidelity parameter k alters the shape of the guarding curve: if females seek extra-pair paternity very actively (high k), guarding time t needs to be close to 100% ($t = 1$) before paternity approaches its maximum. When k is small, much smaller levels of guarding are sufficient to yield high paternity. We call k 'female infidelity', but it must be noted that it does not necessarily reflect observed levels of extra-pair paternity: the latter results from an interaction between k (female behaviour) and mate guarding (male behaviour). Therefore, $k_2 > k_1$ does not mean that we assume *a priori* that less attractive males will achieve less within-pair paternity, rather, they will achieve less if they do not compensate for their unattractiveness by guarding more.

The parameter g in equations (1a and b) measures the efficiency of mate guarding. Small values of g imply that paternity improves slowly with increasing guarding effort. The difference between models (1a) and (1b) lies in the shape of paternity increase. In (1a), males can achieve full paternity if they guard full time, but g determines how quickly this goal is reached (figure 8.1a). In (1b), we assume that males cannot achieve full paternity even if they guard full time: $g < 1$ for this equation (figure 8.1b).

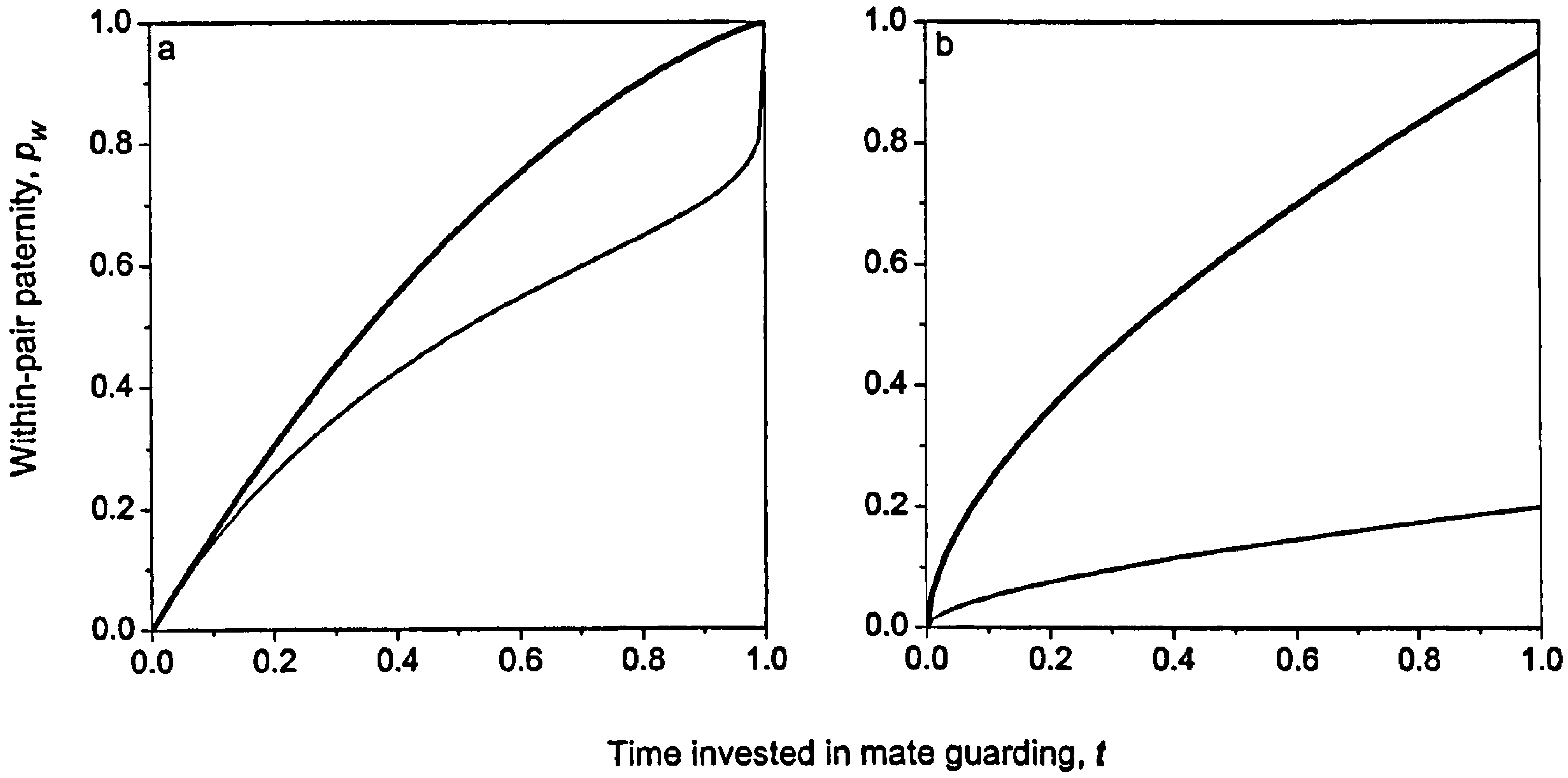


Figure 8.1: Model assumptions regarding within-pair paternity p_W. (a) Model (1a) where 100% guarding time will lead to full paternity. The effect of the guarding efficiency is illustrated with two values of g (thick line, g = 1.2, thin line, g = 0.2). Other parameters: k = 1.2, t_{pop} = 0.5. (b) the alternative model (1b), where males do not achieve 100% paternity even if they guard full time. The effect of the guarding efficiency is illustrated with two values of g (thick line, g = 0.95, thin line, g = 0.2). Other parameters: k = 1.2, t_{pop} = 0.5.

The parameter c_{pop} measures the competitive pressure from other male members of the population, which is a decreasing function of their mate-guarding effort t_{pop}. $c_{\mathrm{pop}} = x\,(1-t_{\mathrm{pop1}}) + (1-x)\,(1-t_{\mathrm{pop2}})a$ describes the average competitiveness of a population member, when the population strategy of guarding is attractiveness-dependent, $\{t_{\mathrm{pop1}}, t_{\mathrm{pop2}}\}$. The parameter a measures how efficiently the unattractive males compete for mates in extra-pair situations, compared with attractive ones ($0 < a < 1$). In case of no quality variation, we set $a = 1$, which yields $c_{\mathrm{pop}} = 1-t_{\mathrm{pop}}$.

In order to make our model self-consistent, paternity needs to sum such that every offspring has one father (Houston & McNamara 2002; Kokko & Jennions 2003). This is achieved by first calculating the population-wide average paternity at home. This equals $p_{\mathrm{Wpop}} = x\,p_{\mathrm{W}}(t_{\mathrm{pop}}, k_1) + (1-x)\,p_{\mathrm{W}}(t_{\mathrm{pop}}, k_2)$, where either equation (1a) or (1b) is used to calculate $p_{\mathrm{W}}(t,k)$. Note that if males do not vary in quality, $x = 1$ and the equation simplifies accordingly.

Thereafter, we express extra-pair paternity for the focal male as

$$p_{\mathrm{E}}(t) = (1-p_{\mathrm{Wpop}})\,c/c_{\mathrm{pop}} \qquad (2)$$

Here, $1-p_{\mathrm{Wpop}}$ is the paternity (per brood) available for extra-pair males, and c/c_{pop} is the competitiveness of the focal male in getting a share of this paternity, relative to average members of the male population. If males do not vary in quality, the share simply depends on the time a male spends not guarding: $c/c_{\mathrm{pop}} = (1-t)/(1-t_{\mathrm{pop}})$. If quality does vary, $c = 1-t_1$ for attractive males whose guarding time equals t_1, and $c = (1-t_2)a$ for unattractive males who guard the amount t_2. c_{pop} is as defined above. Fitness is equal to the sum of paternity at home and elsewhere and the evolutionarily stable guarding time t^* is obtained by creating pairwise invasion plots (see e.g.

Dieckmann 1997 for the exact procedure). In cases where males vary in attractiveness, the game is solved by numerically seeking the values $t_{1,\mathrm{pop}}$ and $t_{2,\mathrm{pop}}$ for which no other t_1 or t_2 can lead to increased fitness, $p_W(t_i)+p_E(t_i)$, for either type of male (i=1, 2). The numerical procedure is simple, as the region of biologically feasible values for t is constrained, $0 \quad t \quad 1$, thus allowing to check all combinations of $\{t_1, t_2\}$ values, with accuracy as desired. We computed solutions with an accuracy of 0.005.

Results

Guarding intensity might be expected to increase with the tendency of females to seek extra-pair copulations (k). However, it turns out that this is not necessarily the case: the relationship is nonlinear, and depends on the particular assumptions made regarding the shape of the trade-off between guarding and extra-pair activities. Mate-guarding behaviour is most intense when it is efficient (i.e. high g), but the effects of female infidelity vary depending on the exact assumptions made (figure 8.2a and b). The paternity function (1a) predicts less guarding when females have a strong tendency for infidelity (figure 8.2a). The function (1b), on the other hand, predicts an initial increase in guarding time with increasing infidelity, and then a decrease (figure 8.2b).

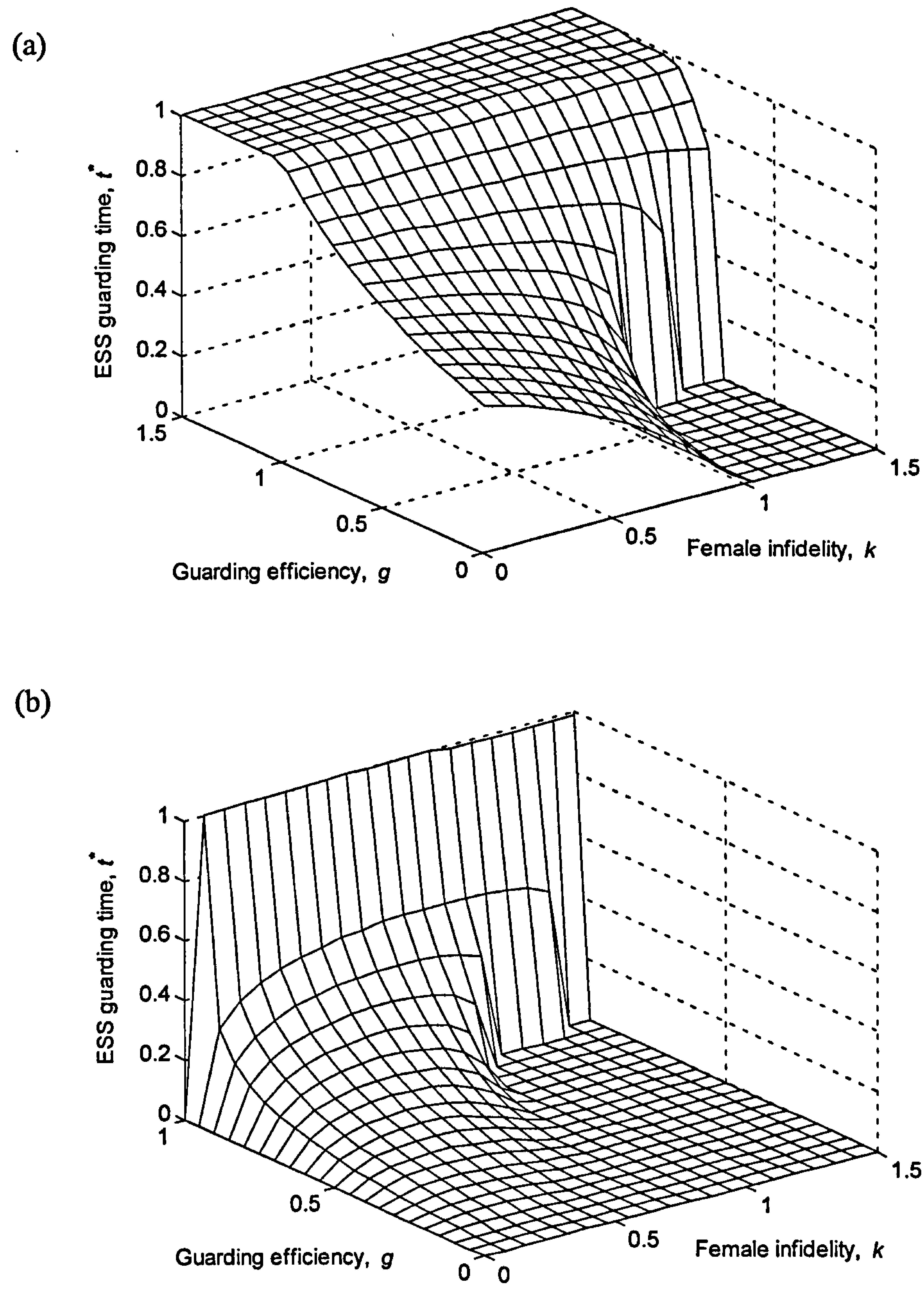


Figure 8.2: Evolutionarily stable mate guarding effort as a function of female infidelity k and mate guarding efficiency g, with within-pair paternity obeying (a) equation 1a, or (b) equation 1b. Note that responses to infidelity differ between model assumptions. All males are assumed to be of equal quality ($a = 1$, identical k values among males).

Males that behave optimally clearly trade off the fitness gains obtained at home with gains elsewhere. If females never seek extra-pair copulations, the time invested in guarding does not have any fitness consequences for the male, and is selectively neutral. With increasing infidelity, the importance of mate guarding increases, but so does the lost opportunity cost of mate guarding. This is because higher female infidelity implies higher potential fitness benefits to the male, provided by extra-pair females. Additionally, the net efficiency of mate guarding deteriorates when females seek extra-pair activities very intensely, and this explains why mate guarding becomes less intense, or vanishes, at high values of *k*.

When males vary in their ability to attract extra-pair females and ensure paternity at home, further complications are possible. Observed within-pair paternity levels arise through an interaction between the tendency of females to seek extra pair mates and the guarding behaviour of males. A typical result of this interaction is that attractive males guard less than unattractive males (figure 8.3): being attractive both improves the paternity a male gains at home gained when he guards little, and enhances his success when he spends time elsewhere (equations 1 and 2). In some cases (figure 8.3a, low to moderate *k*), unattractive males spend all their time mate guarding, and forego the chance of any extra-pair paternity. For attractive males, the trade-off is different: higher chances of gaining paternity away from home, together with their social mate being less inclined to seek extra-pair offspring, means that the optimal time attractive males spend guarding is smaller.

However, this argument does not always hold, due to possible nonlinear relationships between time spent guarding and its effectiveness in deterring extra-pair activities. With high values of female infidelity (*k*) in figure 8.3a and b, unattractive males are not able to secure much paternity at home regardless of their guarding effort. Consequently they may guard less than attractive males, or cease guarding altogether. Attractive males may still spend some time guarding; unless infidelity k increases further to make guarding inefficient for these males too (figure 8.3b).

The exact patterns clearly depend on how a male's attractiveness influences his success at securing paternity at home versus elsewhere. Despite these complications, attractive males are often predicted to guard less, given their higher success outside the pair bond. Does this also mean that they gain less paternity at home, or is reduced guarding fully compensated by their attractiveness (such that their social mate does not tend towards infidelity as strongly as females of other males)? The former possibility predicts that within- and extra-pair paternity gained by a male should correlate negatively, whereas the latter predicts a positive relationship.

Our model predicts that either scenario is possible. In the example of figure 8.3a, compensation is nowhere near complete: attractive males suffer from lower within-pair paternity when they spend less time mate-guarding than unattractive males, except for a small region at high infidelity values where guarding times are almost identical. They enjoy much higher extra-pair paternity, however. Interestingly, they are only able to cuckold other attractive males, as unattractive males spend 100% of their time guarding, which totally protects their within-pair paternity interests. In figure 8.3b, on the other hand, we have assumed that full-time guarding does not guarantee full paternity. Consequently, guarding is less intense, paternities are more evenly distributed, and attractive males win on both fronts: they gain more paternity both at home and elsewhere.

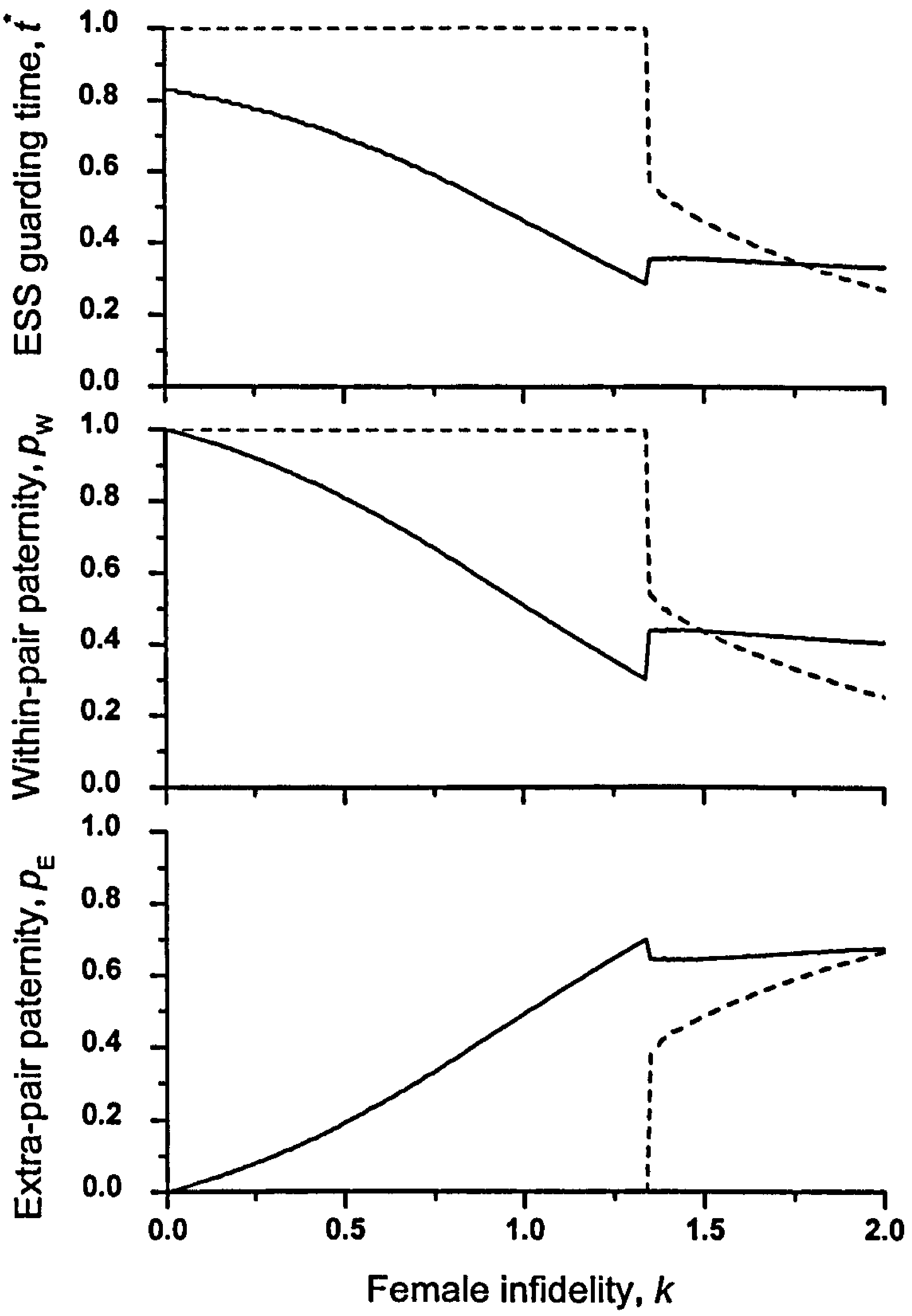


Figure 8.3a: The impact of increasing female infidelity (k) on the evolutionary stable proportion of time invested in guarding, within-pair paternity, and extra-pair paternity, with within-pair paternity calculated according to equation 1a. Solid lines show time invested and paternity gained by attractive males, broken lines show guarding time and paternity gained by unattractive males. Parameter values used: $x = 0.5$, $g = 0.8$, $a = 0.9$, $k_1 = k$ as indicated on the x axis, $k_2 = 2\ k$

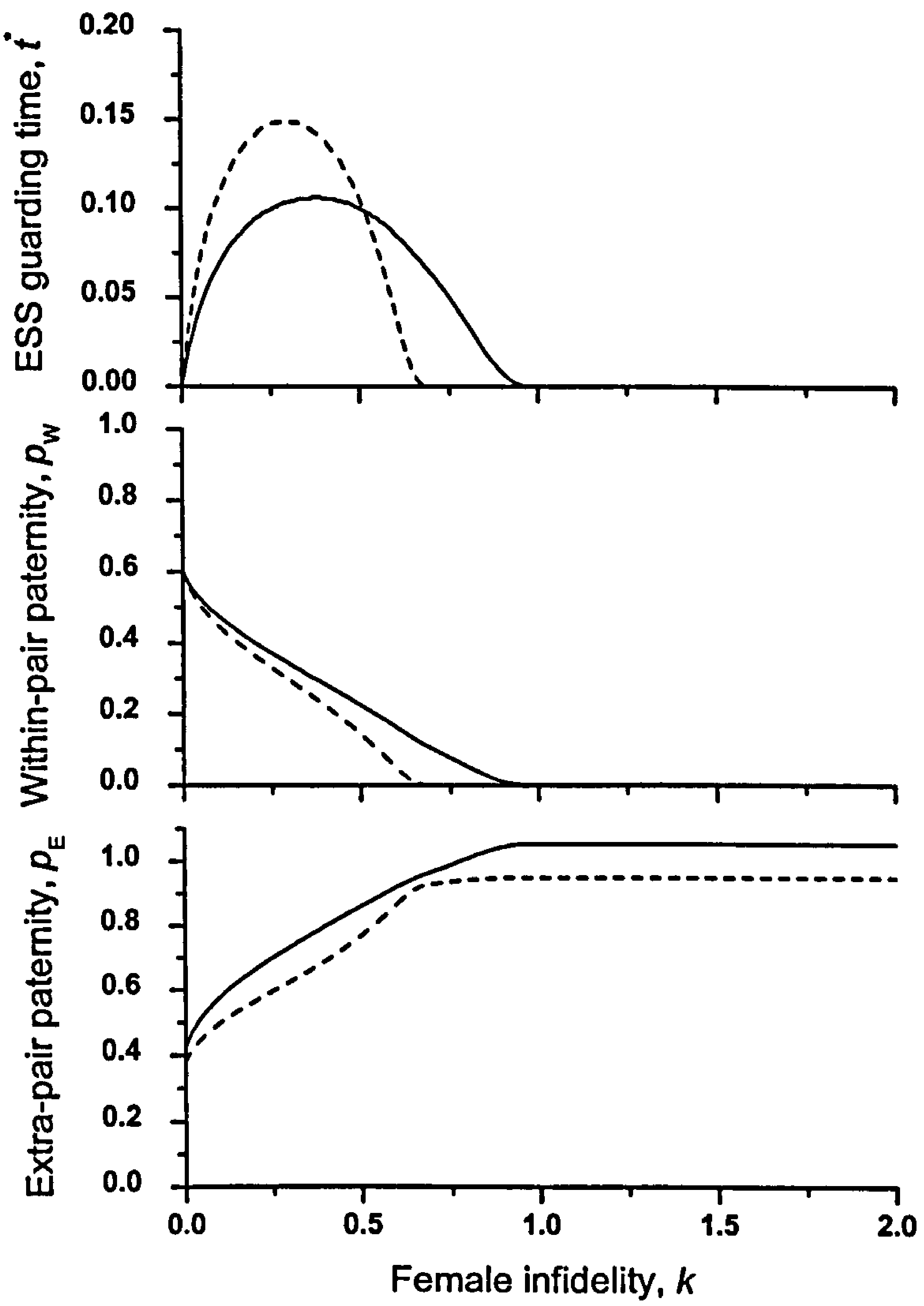


Figure 8.3b: The impact of increasing female infidelity (k) on the evolutionary stable proportion of time invested in guarding, within-pair paternity, and extra-pair paternity, with within-pair paternity calculated according to equation 1a. Solid lines show time invested and paternity gained by attractive males, broken lines show guarding time and paternity gained by unattractive males. Parameter values used: $x = 0.5$, $g = 0.6$, $a = 0.9$, $k_1 = k$ as indicated on the x axis, $k_2 = 1.5\ k$.

Thus, attractiveness can sometimes compensate for reduced mate-guarding at home, but it does not always do so. This is illustrated by varying the relative attractiveness of unattractive males (figure 8.4). When unattractive males have very low success elsewhere (small a), their guarding becomes so intense that their within-pair paternity improves beyond that of attractive males. As the relative attractiveness of unattractive males approaches that of attractive ones (high a, figure 8.4), the males that gain more extra-pair paternity gain more at home too.

Finally, the sign of the correlation between within- and extra-pair paternity may also depend on the efficiency of guarding, g. In the example of figure 8.5, the higher guarding effort by unattractive males almost perfectly compensates for their social mate's stronger tendency to cuckold them. When guarding is very efficient (high g), it overcompensates, and unattractive males end up with higher within-pair paternity p_W than attractive males). When guarding is less efficient (low g), it under compensates.

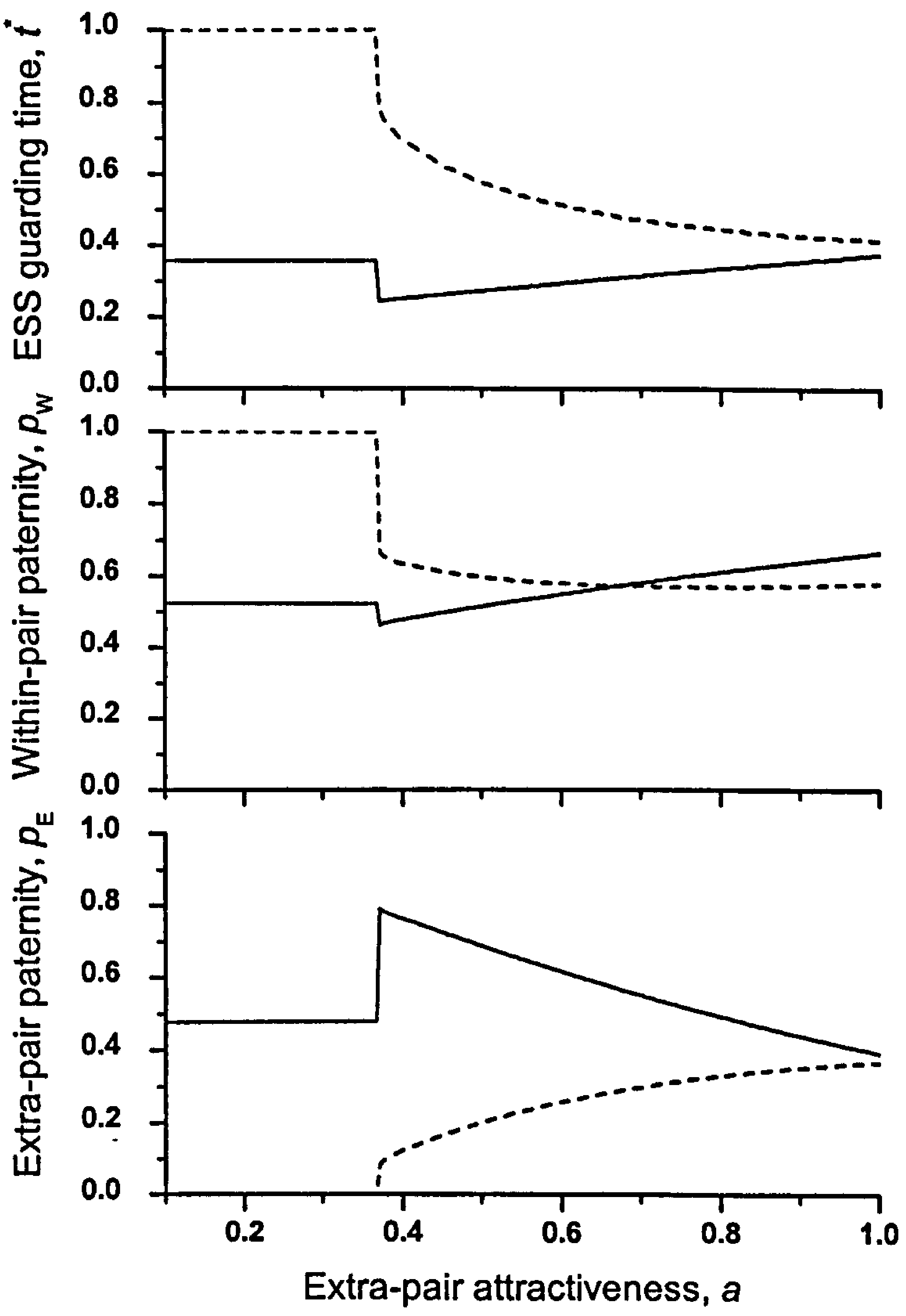


Figure 8.4. Evolutionarily stable guarding times t^*, as well as within- and extra-pair paternity for attractive and unattractive males, as a function a, the relative success of the less attractive males, when they are attempting extra-pair copulations. This example uses within-pair paternity function (1a) with parameter values $x = 0.5$, $k_1 = 0.5$, $k_2 = 0.8$, $g = 0.1$.

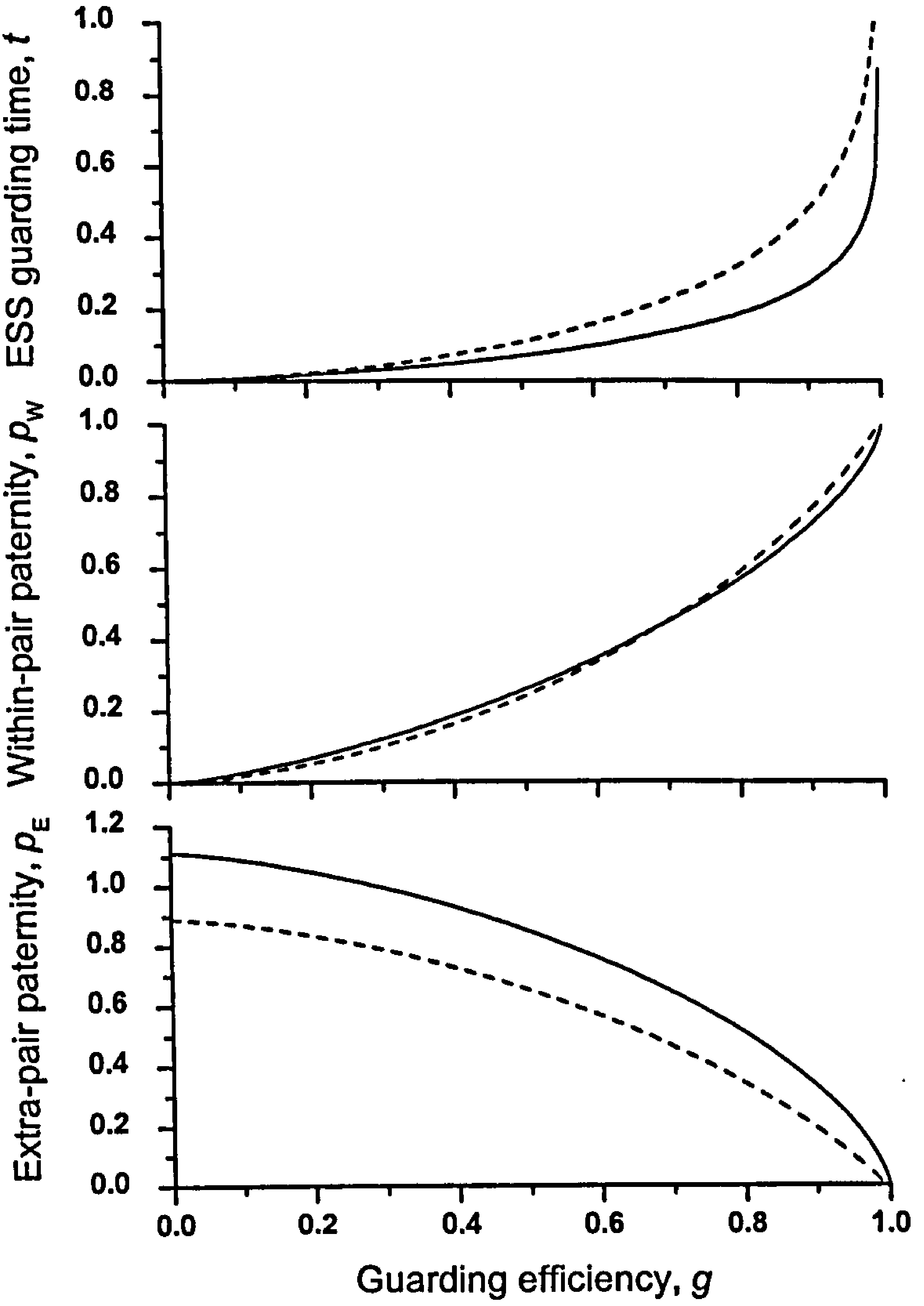


Figure 8.5. Evolutionarily stable guarding times t^*, as well as within- and extra-pair paternity for attractive and unattractive males, as a function of the efficiency of guarding g. This example uses within-pair paternity function (1b) with parameter values $x = 0.5$, $k_1 = 0.3$, $k_2 = 0.4$, $a = 0.8$.

Discussion

Our modelling shows that mate guarding can substantially alter paternity patterns from what would be expected based solely on how much females are assumed to benefit from extra-pair fertilizations. The extent of mate guarding in a particular mating system, however, is difficult to predict for a number of reasons. Firstly, as the female tendency to seek extra-pair copulations increases, there is more reason for the male to mate guard, but at the same time any particular level of mate guarding becomes less efficient, thus forming a disincentive to mate-guard (see Morrell 2004, **chapter 6**, for a related argument in a different context). Secondly, if mate guarding intensity is based on a trade-off between paternity at home and elsewhere, increasing female infidelity implies larger fitness gains for males who spend more time away from home looking for additional matings. This explains why mate-guarding ceases if females become very unfaithful (or very good at escaping male mate guarding attempts), and highlights the importance of taking into account population-level feedbacks in a self-consistent way when developing models of mating systems (Webb et al. 1999; Houston & McNamara 2002; Kokko & Jennions 2003).

The curvilinear relationship between female infidelity and optimal level of mate guarding also complicates the relationship between mate guarding and observed within- and extra-pair paternity. We investigated the consequences of two different biologically feasible relationships between guarding and within-pair paternity, and in both cases the outcomes depend on details such as the efficiency of guarding, and the eagerness of females to seek extra-pair copulations. This may help explain why it is difficult to detect an overall association between mate guarding and paternity in an interspecific comparison (Møller & Ninni 1998). For example, low mate guarding intensity can be equally well predicted under conditions that yield low paternity (guarding is of little use if expected paternity remains low no matter how much the male guards) or under conditions that yield high paternity (if females do not gain much benefit from extra-pair offspring, there is little need to guard, as suggested for the purple sandpiper, Pierce & Lifjeld 1998). Across species, least mate guarding occurs in highly polygynous taxa (Møller & Birkhead 1991), which fits in well with our results that predict cessation of mate guarding at highest values of infidelity k.

If females vary in their behaviour depending on the attractiveness of their mate, we can also expect complications in the relationship between male attractiveness and his paternity with his social mate. Attractive males are often predicted to guard less in our model, yet an attractive male does not necessarily suffer a great fitness loss through cuckoldry in his own nest, if his attractiveness makes his social mate less prone to mate with extra-pair males. However, in other cases we predict that unattractive males guard so much more intensely than attractive males that the within-pair paternity of the latter remains smaller. Such cases are reflected as a negative correlation between paternity at home and elsewhere, and we predict this to be particularly likely when variation in male attractiveness is high (low a in the model), and when females do not pay disproportionate attention to their own social mate's attractiveness when 'deciding' whether to engage in extra-pair activities. Another requirement for a negative correlation is that mate guarding is sufficiently efficient to limit free expression of female mating preferences, since this allows the inferior males to maintain high within-pair paternity.

Is there evidence supporting our result that it can sometimes pay attractive males to reduce mate guarding to such a degree that their paternity at home suffers? A meta-analysis (Møller & Ninni 1998) implies that male birds with more extravagant secondary sexual characters generally enjoy higher paternity in their own nests, but this study did not explicitly quantify if the same males also had elevated success elsewhere. Both positive and negative correlations can be found in the literature (Westneat & Stewart 2003). For example, older Bullock's orioles *Icterus galbula bullockii* lost less within-pair paternity and gained more extra-pair fertilisations than did yearling subadult males (Richardson & Burke 1999). Similarly, most extra-pair males in the blue tit *Parus caeruleus* did not lose paternity themselves (Kempenaers et al. 1997), and in this species, poor quality males who guard lose paternity to good quality males despite their more intense mate guarding behaviour (Kempenaers et al. 1995). But in the yellow warbler *Dendroica petechia*, known extra-pair sires were just as likely to be cuckolded themselves as any male in the population (Yezerinac et al. 1995), and for the pied flycatcher *Ficedula hypoleuca*, it has been reported that attractive black males are cuckolded more than brown unattractive ones (Lifjeld et al. 1997) — although these authors did not find mate guarding an adequate explanation for the pattern. Only a handful of studies exist that document relationships between male mate guarding and other aspects of the mating system. Black-throated blue warbler *Dendroica caerulescens* males with many extra-pair opportunities have been shown to guard less and consequently end up with less paternity in their own broods (Chuang-Dobbs et al. 2001), while in wheatears *Oenanthe oenanthe*, good body condition seems to aid paternity at home as well as improving success elsewhere (Currie et al. 1999).

In the example of the wheatear, the positive correlation may be partly explained by adaptive time allocation: males guard intensely when the female is close to laying (Currie et al. 1998), which may allow the best males to escape the strict trade-off and achieve high paternity at home as elsewhere. In our model, we assumed that males could not escape the trade-off; if they do so (at least partly), the likelihood of positive correlations between within- and extra-pair paternity will increase. In any case, late breeding wheatears are documented to use direct guarding more than early breeding ones (Currie et al. 1998), a pattern predicted by our study if the early arriving birds are better competitors (Kokko 1999). Similarly, in penduline tits *Remiz pendulinus* — a species in which neither mate guarding nor cuckoldry is particularly intense — males who guarded most were more likely to suffer cuckoldry (Schleicher et al. 1997).

The extent to which female choice for extra-pair fertilizations is restricted by mate guarding requires much more study. The above results give the impression that examples where less attractive males gain more paternity at home (due to extensive and efficient mate guarding) are quite rare. If this proves to be true generally, mate guarding does not appear a very strong evolutionary force in shaping mating systems. But if females regularly escape mate guarding attempts, we face an enigma: why does mate-guarding evolve, if it is so inefficient? Currently, we do not have a general answer to this question. Studies on paternity rarely present data in a form that allows direct comparison of within- and extra-pair paternity, and direct data on mate guarding is usually lacking. Such data are crucial before general conclusions can be made about the importance of mate guarding in shaping genetic parentage in socially monogamous species.

Thus, we can only point to a surprising lack of knowledge on natural systems regarding the various theoretical possibilities: the relationship between male attractiveness and mate-guarding may mean that sexual selection uniformly favours attractive males both in their own brood as well as elsewhere, or, alternatively, less attractive males perform relatively well under social monogamy, due to their mate guarding efforts. In the latter case, mate guarding diminishes the intensity of sexual selection arising through female choice. Even in the cases where mate guarding can be shown to be efficient in restricting female infidelity (as has been shown experimentally for the Seychelles warbler *Acrocephalus sechellensis*, Komdeur et al. 1999, and black-throated blue warblers, Chuang-Dobbs et al. 2001), between-individual variation can allow for a variety of different relationships between guarding and paternity. These patterns remain to be investigated in wild populations, as do those that arise from the interaction between mate guarding and alternative paternity guards, such as frequent copulations (Møller & Birkhead 1991).

CHAPTER 9

GENERAL DISCUSSION

Game theory approaches have been applied to a wide range of evolutionary questions (Nowak & Sigmund 2004), including animal behaviour, resource allocation in plants (Falster & Westoby 2003), arms races between predators and prey (Abrams & Matsuda 1997) and the acquisition of language in humans (Nowak et al. 2002). Game theory models of animal behaviour have provided a strong framework for explaining many aspects of behaviour in terms of the costs and benefits to the individual, from co-operation (e.g. the Prisoners Dilemma; Axelrod & Hamilton 1981) to conflict (e.g. the hawk-dove game; Maynard Smith & Price 1973). Models of animal behaviour can only be of practical use in behavioural ecology if:

- Their predictions can be tested using empirical systems, in order to determine whether the underlying assumptions are accurate. For example, the duration of fights decreases with increasing size asymmetry between the contestants (e.g. Englund & Olsson 1990; Pratt et al. 2003, see **chapter 2**), as predicted by the sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984), or

- They can explain existing patterns in the data. For example, an explanation for the observation that in territorial contests, owners tend to win, was provided by the hawk-dove game, where 'bourgeois' (attack if resident, retreat if hawk) was an ESS (Maynard Smith & Parker 1976), or

- They are used to investigate the underlying assumptions of other types of models, such as mechanistic approaches. For example, the assumptions of mechanistic models of movement and scent marking in wolves (Lewis &

Murray 1993; White et al. 1996) have been tested using a game theoretic approach (Lewis & Moorcroft 2001).

In this thesis I have used and developed a number of game theory models to investigate aspects of conflict resolution in animals, and have aimed to either test the predictions of existing mechanistic models, or provide testable predictions.

In **chapter 2**, I tested the predictions of existing models of territorial contests. Although many models of animal conflict exist, there are many further avenues of research emerging, and it is unlikely that a single model can be applicable to all species and situations. Researchers have developed several different models of animal conflict, aiming to predict the outcome, duration and in some cases the sequence of behaviours occurring during a fighting. These are outlined in **chapter 1** and discussed in **chapter 2**. However, determining which of these models is applicable to different situations can be difficult. The sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990) and war of attrition (Parker & Rubenstein 1981; Hammerstein & Parker 1982) assume that mutual assessment of opponents occurs during conflict, and makes predictions regarding duration on the basis of that assumption. The energetic war of attrition (Payne & Pagel 1996, 1997; Payne 1998) and the war of attrition without assessment (Mesterton-Gibbons et al. 1996) assume that no such assessment needs to occur, and yet make similar predictions about fight duration.

Taylor and Elwood's (2003) recent investigation of these different game theory models of conflict duration suggests that many studies of fight duration may have involved incorrect interpretation of the data, due to the similar predictions of these different models. They presented a framework for the analysis of fighting duration which attempts to distinguish between different models, and therefore to determine which of the underlying assumptions are applicable to a particular species. In **chapter 2,** I investigated the duration of fighting in fiddler crabs (*Uca mjoebergi*), in order to determine whether contest duration was a results of individual thresholds reached first by the loser, or by the loser assessing its relative inferiority and deciding to retreat. Finding that neither of the hypotheses investigated by Taylor and Elwood (2003) provided a good description of fighting duration in this species, I further developed their framework incorporating an alternative game theory model - the cumulative assessment game (Payne 1998, see **chapter 1**). **Chapter 2** highlighted the difficulty of distinguishing between different models of fighting behaviour, and provided an alternative explanation for the patterns seen.

The cumulative assessment model and the sequential assessment game both make predictions as to the sequences and rates of actions the contestants employ during a fight. For example, the sequential assessment game predicts that actions should increase in intensity during the fight (Enquist et al. 1990), while the cumulative assessment game allows for de-escalation to occur (Payne 1998). It is clear that further detailed studies of fighting behaviour are needed to accurately determine which models of fighting provide the best description of the behaviour observed in *U. mjoebergi* and other species.

It has already been suggested that much data on fight duration needs to be reanalysed (Taylor & Elwood 2003; Gammel & Hardy 2003), since many researchers have failed to investigate the possibility that duration is determined by individual thresholds and predicted by the size of the loser. Instead, much previous work has concentrated on investigating relative size as a predictor of duration and found support for mutual assessment of relative size. The findings of **chapter 2** suggest that individual thresholds are important, supporting the call for reanalysis.

In the study of fighting in fiddler crabs (**chapter 2**), fighting was size assortative, with intruders selecting opponents that were of similar size to themselves, but I observed cases in which small males were aggressive towards larger males, when they were both intruders and owners. Aggressive behaviour directed towards a larger opponent has been noted in many species (Dow et al. 1976; Enquist & Jakobsson 1986; Ribowski & Frank 1993; Smith et al. 1994; Morris et al. 1995; Moretz 2003), and there are a number of explanations as to why this might be the case. In **chapter 3**, I discussed these reasons, and developed a model in which the individuals could accurately assess their chances of winning (to remove the possibility that perception errors cause misdirected aggression; Bradbury & Vehrencamp 1998; Just & Morris 2003), and the resource was of equal value to both competitors (to remove the possibility that smaller individuals value the contested resource more highly; Davies & Houston 1981; Shutler & Weatherhead 1992; Eason & Hannon 1994; Johnsson et al. 2000; Johnsson & Forser 2002). I found that small individuals are predicted to attack large ones when they have some chance of winning and the probability of finding an alternative, uncontested resource is low. Thus, aggression can be expected when body size does not perfectly determine outcome and individuals have few alternative options (the desperado effect; Grafen 1987).

In addition, the model in **chapter 3** predicted that low intensity aggression (displays) by a small individual could result in a retreat response from a larger opponent. In this situation, small individuals would appear more aggressive than their larger opponents. This has some similarities to the paradoxical strategies discussed in **chapter 1**, and investigated in **chapters 4** and **5**. This ESS coexisted with a common-sense alternative, where large individuals display and small individuals retreat. It was predicted to occur when the competitors had many alternative options for gaining access to resources, and when the smaller competitor had a good chance of winning, suggesting that aggression is not worthwhile, and either competitor may retreat in these circumstances. Opportunities to extend this chapter include asymmetries in the value of the resource to the two contestants (Shulter & Weatherhead 1992; Eason & Hannon 1994), and asymmetries in the costs paid by them (Zahavi 1975; Neat et al. 1998a; Maan et al. 2001). This could potentially lead to a wider range of ESSs than found in **chapter 3.**

Although the different game-theory models of fighting are supported in various species, they generally consider pair-wise interactions between individuals fighting over an indivisible resource such as a territory, and assume that the resource can only be gained after winning a fight. Stamps and Krishnan (1999, 2001) developed a mechanistic model of fighting behaviour suggesting that in cases where resources are divisible, for example, when newly settled individuals are dividing an area of habitat into territories, space can be won through 'nagging': repeated low cost interactions with the same individual, and through a tendency to avoid places where those interactions have occurred (Sih & Mateo 2001). In **chapters 4** and **5**, I used modelling approaches to test the hypothesis that avoidance of fight locations can lead to the acquisition of space, firstly in a one-dimensional context (**chapter 4**) and then two-dimensionally (**chapter 5**) where space was modelled explicitly.

In **chapter 4**, I found that both Stamps and Krishnan's (1999, 2001) hypothesis, and the winner-takes-all assumptions of some game theory models (Maynard Smith & Price 1973; Grafen 1979; Maynard Smith 1982) were supported, but under different parameter values, and therefore different assumptions about the costs and benefits of fighting. Avoidance of areas where fights have occurred can be adaptive, but only if the benefits associated with access to the resource are low compared to the costs of fighting. Otherwise, one individual (typically the winner) responds by returning to the contested area while the other (the loser) avoids it, and space is gained by winning fights.

While game theory approaches can be used to test the assumptions of mechanistic models, there is an important difference between these two approaches. Mechanistic models, which describe animal movements, tend to be spatially explicit in two dimensions and thus in some ways more realistic than game theory models, in which space is not modelled explicitly (Parker & Knowlton 1980), or modelled only in one dimension (Maynard Smith 1982; Lewis & Moorcroft 2001; Mesterton-Gibbons & Adams 2003; Pereira et al. 2003). It may be appropriate in some cases to consider whether the predictions of game theoretical approaches hold up under a spatially explicit treatment. **Chapter 5** represented an attempt to bridge this gap between existing mechanistic and game theoretical models of space acquisition.

Chapter 5 also considered whether avoidance of fight locations is adaptive, but in two-dimensional space. This chapter supported the findings of **chapter 4**: when the costs of fighting were high relative to the benefits of using the resource, the most adaptive behaviour was to use an avoidance strategy, and this led to the formation of well-defined, exclusive territories. **Chapter 5** also considered the effect of population density. Adaptive avoidance behaviour and exclusive territoriality were predicted to occur when populations exist at low densities. **Chapter 5** predicted that high densities (and low fighting costs) lead to the breakdown of territoriality and the formation of large overlapping home ranges. Thus, while I was able to show that avoidance behaviour could be adaptive in **chapter 4, chapter 5** demonstrated that, of the strategies investigated, only the avoidance strategies could lead to the formation of territories, while supporting the findings of **chapter 4**.

In the wild, territory size tends to vary with body size (e.g. Schoener 1968; Petrie 1984; Hart 1987; Keeley & McPhail 1998; Keeley 2000), resource abundance and intruder pressure (see Adams 2001 for a review). **Chapter 5** provides another possible observation to explain variation in territory size among individuals: even though all individuals were of equal fighting ability, and the habitat was homogeneous, territory sizes varied between individuals. This is because territory expansion for each individual began from a randomly selected location, and for some individuals, this may not be the most favourable location (for example, it may have several near neighbours).

Game theory models of fighting behaviour often show that a paradoxical alternative to the common-sense solution is stable under at least some of the parameter values investigated (Maynard Smith 1974; Maynard Smith & Parker 1976; Enquist & Leimar 1987; Mesterton-Gibbons 1992; Mesterton-Gibbons & Adams 1998). However, apparently paradoxical strategies are extremely rare in nature, and may not be paradoxical at all when other factors are taken into account. For example, Hernandez and Benson (1998) found that in territorial contests between male *Heliconius sara* butterflies, smaller males tended to win, suggesting a paradoxical strategy. However, in this species, large male have less to gain from holding a territory as they are better able to compete for females at pupal emergence sites (Field & Hardy 2000; Kemp 2000), leaving small males to make the 'best of a bad job' and defend territories. Thus, small males may have more to gain from winning, and hence be prepared to fight harder. This represents a common-sense solution to the problem (**chapter 1**). While paradoxical solutions remain a feature of some game theory models, their absence in nature (or presence within a modelling framework) needs to be explained before the models can truly be said to accurately represent nature. **Chapters 4** and **5** investigated whether a paradoxical solution for the division of space (rather than in winner-takes-all fights that were the focus of early game theory models; Maynard Smith & Parker 1976; Hammerstein & Parker 1982; Enquist & Leimar 1987) can be evolutionarily stable. In **chapter 4**, I found that paradoxical solutions can only persist when asymmetries are small, and cannot evolve from a common-sense ancestral population strategy. These findings are in line with the occurrence of paradoxical strategies in early hawk-dove games, where the paradoxical strategy tends to have a smaller basin of attraction in comparison to the common-sense alternative (Maynard Smith & Parker 1976). Additionally, in **chapter 4**, I found that paradoxical strategies were found only when animals adhered strictly to behavioural rules. When incorporating 'errors in decision making', individuals may choose the option that leads to lower fitness, if the fitness difference is small (McNamara et al. 1997). Using this method has two potential benefits. Firstly, a common problem with the iteration of the best response map technique, often used to find the ESS (McNamara et al. 2000) is that the sequence of strategies sometimes oscillates without converging to an ESS, and by incorporating errors, oscillation can be eliminated. In addition, incorporating errors can increase the biological realism of game theory models.

Game theory models of fighting behaviour tend to assume that, for a given individual, a fight can only end with one of two possible outcomes: a win or a loss (Maynard Smith & Parker 1976; Enquist & Leimar 1987; Hammerstein & Parker 1982; Mesterton-Gibbons 1992). However, in nature, some fights may end without a clear winner and loser, ending instead in a stalemate or draw (Bleistein et al. 1994; Stamps & Krishnan 1994a, b, 1997, 1998; Adams 1998; Stamps 1999; Draud et al. 2004). Although draws were incorporated into the model of **chapter** 4, their importance was not investigated. **Chapter 5** investigated the importance of draws in determining the stability of common-sense versus paradoxical strategies. In contrast to earlier models that ignore draws, I defined the paradoxical strategy to include the opposite responses to draws compared to the response of the common-sense strategy. When this difference was taken into account, I found that when draws occurred relatively uncommonly the common-sense and paradoxical strategies behaved similarly, but when draws occurred commonly (as occurs during the division of space; Stamps & Krishnan 1999), the common-sense strategy was more often adaptive than the paradoxical alternative.

There are many previously modelled aspects of fighting and territoriality that were not incorporated into **chapters** 4 and 5, but would present interesting avenues for further research. In addition, **chapters** 4 and 5 present some techniques that could be incorporated into other models. Opportunities for further work on the acquisition of territories include:

- In **chapter 5**, all individuals were assumed to be equal in terms of their RHP. Stamps and Krishnan (2001) incorporated asymmetries between individuals into their model of spatial division, and found that stronger individuals ended up with larger territories, as they suffered lower costs of fighting and so were less deterred from returning to areas where they had been involved in fights. Asymmetries between individuals (as in **chapter 4**) could be incorporated into models investigating the adaptiveness of strategies in a two-dimensional context. This would allow for investigation of the resulting territory size, and whether different strategies were adaptive for individuals of differing RHP.

- Prior experience of winning and losing can be important in determining the outcome of fights (the winner-loser effect, Dugatkin 1997; Hsu & Wolf 1999; Johnstone & Dugatkin 2000; Dugatkin & Earley 2004). Where sequences of fights occur, this could be incorporated, and it might lead to effects such as the winners of fights ending up with larger territories, even when they do not differ in fighting ability (RHP).

- An interesting case for further development of **chapter 5** would be the inclusion of landmarks and habitat heterogeneity. Territory size and shape known to be influenced by factors such as the availability of perch sites (Yosef & Grubb 1994), the visibility of areas that must be defended (Eason & Stamps 1992), the space use of potential mates (Butchart et al. 1999) and the occurrence of landmarks. Landmarks can be used as conventions dictating the boundaries of territories, and therefore reducing the frequency of aggressive encounters (Eason et al. 1999; LaManna & Eason 2003; Mesterton-Gibbons & Adams 2003). Investigating the limits of such conventions in a two-dimensional setting, and examining the population consequences of landmark usage would be a fruitful avenue of further research.

The later chapters of the thesis considered how individuals should resolve trade-offs between two or more mutually exclusive behaviours. Models of the trade-offs between behaviours tend to focus on specific examples, such as the trade off between parental care and seeking additional mating opportunities (Magrath & Komdeur 2003), and thus there is much scope for investigating how behaviours trade off in different systems.

Houston and co-workers (2003) showed that differences in individual quality can produce counter-intuitive patterns of optimal behaviour, when there is a trade-off between survival and reproduction, and when fitness can be written in the form of a product of these two behaviours. The possibility that one behaviour is an essential prerequisite to the other (i.e. fitness is not simply a product of the two behaviours) is incorporated into **chapter 6**. In an optimality approach, I showed that the counter-intuitive pattern is seem only when an individual's ability to perform the second (less essential) of the behaviours is altered. Understanding that models predict counter-intuitive patterns of behaviour may be essential if we are to fully understand trade-offs that are seen in nature, and in **chapter 6** I made some suggestions as to how empiricists could investigate the patterns that I predicted. **Chapter 6** presented a general model that does not provide an accurate description of any particular study system, but could be adapted to make it more specific. For example, in a trade-off between territorial defence and mate attraction, females may gain information on a male's quality as a mate from observing his defensive behaviours (e.g. Gronstol 1996), or from the quality of the territory he is defending (Real 1991; Reynolds 1993), and the trade-off may therefore be different from that predicted in **chapter 6.**

Optimisation models of territory size (e.g. Hixon 1980; Ebersole 1980; Schoener 1983; Hixon 1987; McNair 1987) assumed that intruders arrived at random and owners could expel them if they choose to do so (Adams 2001). In reality, however, territories are likely to be constrained by the presence of neighbours holding contiguous territories (Hixon 1980; Grant 1997; Adams 1998; Keeley 2000), and other approaches, including game theory, were needed to describe how boundary locations result from the interaction of individuals (see **chapter 5**). A territorial male may spend some time intruding onto neighbouring territories, or interrupting the courtship of other males, and his own defensive effort may depend to some extent on the amount of time his neighbours spent doing the same thing. A further avenue of research into the trade-offs between behaviours (discussed in **chapter 6**) would be to adopt a game theoretical approach, as in **chapters 7** and **8**, to investigate how the trade-off between behaviours occurs when the actions of other individuals are taken into account.

The fact that the decisions of others affect the behaviour of a focal animal is central to game theory, and is likely to be important in the optimal resolution of time or energy conflicts. In addition to considering the behaviour of individuals, we also need to consider how the environment experienced by an individual changes according to the behaviour of other individuals in the population. For example, in **chapter 5**, the way in which individuals divided space affected the payoffs available to each one. More generally, resource availability may depend on the behaviour of others. Such an approach was taken in **chapters 7** and **8**, where the optimal decisions of resource-owning males depended on the behaviour of others in the population, and this also affected the payoffs available. In **chapter 7**, I assumed that the activity decisions of male bowerbirds depended on how other males were allocating their time, and this affected the quality of the male's bower. High levels of raiding in a population led to pressure on males to spend more time protecting the bower from competitors, and thus time spent on the bower conflicted with time that could be spent searching for decorations to improve the bower quality, or raiding the bowers of other males, to increase an individual's own bower quality while reducing the quality of his competitors. The model is a simple description of bowerbird behaviour, and data on bowerbird time budgets is scarce, and thus the predictions are difficult to test. Where data are available, the model predicts more time spent on the bower than has been observed. There are a number of reasons why this may be the case, outlined in **chapter 7**, and modification of the model may provide a better fit to the data. For example, the assumptions of the model may not be applicable to all bowerbird species: I assumed, for example, that courtship occurs at the bower, whereas in Regents bowerbirds (*Sericulus chrysocephalus*), courtship begins in the canopy. In **chapter 4**, the likelihood of making errors when choosing the optimal behaviour (McNamara et al. 1997) was important in determining the ESS that was reached (paradoxical or common-sense) and the incorporation of errors in decision making into **chapter 7** could potentially increase the fit between the model and the observed data.

The main finding of **chapter 7** is that increasing female discrimination for mates is predicted lead to deterioration in the average quality of one of their sexual ornaments, in this case, their bowers (additionally, bowerbirds have plumage and behavioural displays; e.g. Coleman et al. 2004). This occurs through a mechanism whereby female discrimination leads to an increase in competition between males in the form of raiding, but may also be applicable to situations where males compete less directly for females. This could provide a natural stopping point for the runaway evolution of male traits, something that open ended models of runaway sexual selection require to be realistic (Kokko et al. 2003). In **chapter 7**, I assumed that all individuals were equal with respect to their bower-building ability, and the model sought the equilibrium bower quality under such conditions. In nature, variation is likely to exist around any trait. In **chapter 7**, I proposed that a decrease in mean trait size could hamper female choice if smaller traits have less perceptible variation around them.

Asymmetries between individuals are known to be important in determining the outcome of contests over territories and food resources (Davies 1978; Krebs 1982; Marden & Waage 1990; Beaugrand et al. 1996; Jennions & Backwell 1996; Chellappa et al. 1999), and the same is likely to be true when males compete for ornamental objects. In bowerbirds, much variation in the quality of bowers has been observed (Borgia 1985, Lenz 1994; Uy & Borgia 2000; Madden 2003), and bowers are known for being extremely elaborate, and females very selective (Uy et al. 2001; Coleman et al. 2004). Incorporating variation in male quality into a future model of bowerbird behaviour could lead to increased variation in bower quality. Competition between males increasing the variance in male sexual ornaments has been noted before: in sticklebacks, competition between males enhances the variation in red colouration, used in female choice (Bakker 1994; Rowland 1994).

Chapter 8 investigated the optimal allocation of time to mate guarding versus seeking extra pair copulations in socially monogamous birds, although the findings are also applicable to mate-guarding mammals. Although there is extensive theoretical work regarding mate guarding in crustaceans and insects (Parker 1974b; Grafen & Ridley 1983; Jormalainen 1998; Härdling et al. 2004), the results from these models are not applicable to all animals: in invertebrates, guarding takes the form of continuous physical contact (amplexus). In mate guarding vertebrates such as birds, males cannot guard their mates in this way and instead do so by maintaining physical proximity to fend off other males and prevent the female from seeking extra-pair copulations. Thus the dilemma facing a male bird is not how long to maintain guarding before seeking a further mate, but how to allocate time to guarding a social mate when extra-pair copulation opportunities are available (Hasselquist & Bensch 1991). Fishman et al. (2003) investigated this problem, and found that an ESS is to guard during the female's fertile period and seek extra-pair copulations outside this time. This strategy, however, is only effective when female fertility is asynchronous within the population. **Chapter 8** investigated the situation where female fertility is more or less synchronous, and found that the behaviour of females and the quality of males were fundamental in determining how males should allocate their time to guarding.

In **chapter 8**, I found that paternity patterns within nests cannot necessarily be predicted by the guarding behaviour of males: paternity should depend strongly on the attention that females pay to the quality of their mate. If females mated to high quality males are less likely to seek extra-pair copulations, then high quality males should have higher paternity in their own nest than low quality males. If however, females are equally unfaithful to both high and low quality males, high quality males should gain lower within-pair paternity, since they are predicted to reduce guarding activity due to the many extra-pair opportunities available to them. In general, it seems that there are few examples where unattractive males gain more paternity at home than attractive ones, but there have been few empirical studies that investigate both guarding behaviour and other aspects of the mating system. In black throated blue warblers, *Dendroica caerulescens*, attractive males with many extra-pair opportunities have been shown to guard less, and as a consequence, end up with lower paternity in their own broods (Chuang-Dobbs et al. 2001). **Chapter 8** provides a previously lacking theoretical framework for the combined empirical investigation of attractiveness, paternity and guarding behaviour. However, the question as to why mate guarding should evolve in socially monogamous birds remains unanswered, and more empirical studies into the relationships between attractiveness, paternity and guarding behaviour are needed before conclusions can be drawn regarding the importance of mate guarding in shaping parentage in socially monogamous species, and the extent to which mate guarding is effective in restricting female infidelity.

Chapters 7 and **8** both investigated the importance of female choice in determining how males should behave, showing female behaviour can have strong effects on the optimal trade-off decisions of males. While this obviously has fitness consequences for the males, it can also feed back and influence the females themselves. In **chapter 7**, increasing female choice led to the deterioration of bowers, which could potentially hamper the ability of the female to choose the highest quality males. Game theory approaches, particularly to modelling conflicts, often only include the sex of interest: if it is males who fight over territories, then the behaviour of a male is presumed to depend only on the behaviour of other males. **Chapters 6** and **7** highlight the importance of considering the behaviour of individuals not under direct consideration when developing game theory models.

Developments in game theory

There have been a number of recent developments in game theoretical techniques, which have the potential for increasing our understanding of animal behaviour and providing better matches for observed data where this is required. These techniques provide useful avenues of research in game theoretical modelling of different systems, some of them have been included in the models in this thesis, and others could potentially be used to extend the work presented here.

- *Self-consistency in game-theory modelling.* In one of the classic models of parental care (Maynard Smith 1977), males gain offspring that do not appear in calculations of female fitness (Kokko & Jennions 2003). A fundamental constraint, however, is that in sexually reproducing species, each offspring must have exactly one mother and one father (Houston & McNamara 2002). Such conservation of paternity has been shown to have important implications for the caring decisions of males and females (Queller 1997, Kokko & Jennions 2003), and the principles of self-consistency should be incorporated into game theory modelling (as in **chapter 8**).
- *Coevolution of male and female behaviours.* In **chapters 7** and **8**, male behaviour was free to evolve, while female behaviour was fixed. In reality, females too should be free to respond to changes in male behaviour: the optimal behaviour for a male should depend on the behaviour of females, and

vice versa (Houston & McNamara 2002; Kokko et al. 2003; Hall et al. 2000). In the example of **chapter 8,** if males evolve to guard their females more intensely, then females aiming to gain extra-pair copulations should evolve behaviours that allow them to escape the males' paternity guards.

- *Negotiation.* The standard approach in two-player games is to assume that each individual chooses the best response to the behaviour of its opponent. McNamara et al. (1999) suggest that an alternative approach is to view such games as a negotiation between the opponents, where each individual seeks the evolutionary stable negotiation rule rather than the evolutionary stable action. This approach has been applied in models of parental effort (McNamara et al. 1999; McNamara et al. 2003), and in the evolution of cooperative behaviour (Taylor & Day 2004). The resolution of conflicts through negotiation would be an interesting development of some chapters in this thesis.
- *Variation in behaviour.* The standard solution to the Prisoners' Dilemma game (Axelrod & Hamilton 1981) is that the only ESS is mutual defection. McNamara et al. (2004) recently showed that if there is variation in behaviour, maintained by external factors such as migration and mutation, then high levels of cooperation could be evolutionarily stable, as there is always some chance that the opponent will cooperate. Potential sources of variation that may promote cooperation also include stochastic strategies, variation between individuals in their quality (McNamara et al. 2004) errors in decision-making (McNamara et al. 1997; incorporated into **chapter 4,** see also Fawcett & Johnstone 2003).

- *Pure and mixed ESSs.* In models of asymmetric contests, where individuals can accurately assess their opponent's ability, Selten (1980) showed that only pure strategies can be stable (as in **chapter 3**). In contrast, when games are symmetrical, mixed strategies (probabilistic behaviour) can exist (Maynard Smith 1982). Recently, Crowley (2000) has shown that if individuals categorise their opponents (same size, larger, smaller), rather than accurately assessing size on a continuum, mixed strategies can be found as solutions to asymmetric games (Crowley 2000, Flaxman 2000). As such, assumptions about whether assessments are discrete (categories) or continuous can have important consequences for our predictions of what we could observe in nature (Flaxman 2000), particularly with respect to fighting behaviour.
- *Unpredictability in behaviour.* Social behaviour such as aggression often appears to be unpredictable, and prevents opponents from developing effective counter-strategies. Kazem and co-workers (2004) have shown that unpredictable punishment of subordinate individuals by dominant ones can be adaptive, as it deters the subordinates from behaviours that draw punishment. Unpredictable behaviour may therefore be important in determining the dynamics of social relationships, and should be considered further.
- *Spatial structure.* It is widely accepted that the incorporation of spatial structure into the Prisoner's Dilemma game leads to the evolution of cooperation that does not exist in the absence of such spatial structure, as neighbours are more likely to cooperate with one another (Wilson 1975). Recent work, however suggests that this may not be the case in a version of the hawk-dove game, known as the snowdrift game, where spatial structure

may reduce the proportion of co-operating individuals (Hauert & Doebeli 2004; Taylor & Day 2004). Thus, spatial structure may change the conclusions of spatially implicit models. In **chapter 5**, the findings of **chapter 4** were supported when space was modelled explicitly, and the spatial approach allowed further questions to be investigated.

- *Social context.* Aggressive interactions between individuals are often modelled as pair-wise interactions, but in reality take place within a social environment, and this may affect the dynamics of current and future interactions. Previous experience of winning or losing can influence future behaviour and success in fights (Dugatkin 1997; Hsu & Wolf 1999), as can 'eavesdropping' on interactions between other conspecifics, where bystanders gain information individuals involved in contests (Johnstone 2001; McGregor et al 2001; Earley & Dugatkin 2002; Whitfield 2002). Finally, third parties may become involved in fights, forming coalitions to defend territories, for example (Getty 1987; Backwell & Jennions 2004)
- *Individual behaviour and population dynamics.* A limitation of **chapter 4** is that population density is a parameter, rather than a consequence of the population dynamics generated by individual behaviour (Eshel & Sansone 1995; Mylius & Diekmann 1995; Kokko & Lundberg 2001). Behaviour-based models of population growth determine the ESS behaviours underlying density dependent processes that effect population dynamics (e.g. territorial behaviour Kokko & Sutherland 1998; see Sutherland & Norris 2002). These models can then be used to make predictions regarding the effects of environmental change on populations, through the responses of individuals to

those changes (reviewed in Sutherland & Norris 2002; Norris 2004), and game theory can provide answers to conservation problems.

In conclusion, game theory has been extremely important in explaining apparently selfish patterns in animal behaviour, and behaviours that do not appear to benefit the individual. The modelling chapters in this thesis have developed new game theory approaches to modelling animal conflict, investigated the trade-offs that occur between behaviours, and provided a number of predictions which can be tested in empirical systems, as well as investigating the adaptive behaviour behind existing observations and mechanistic models.

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