



## Chapter 6

# Modulating Aggression Through Experience

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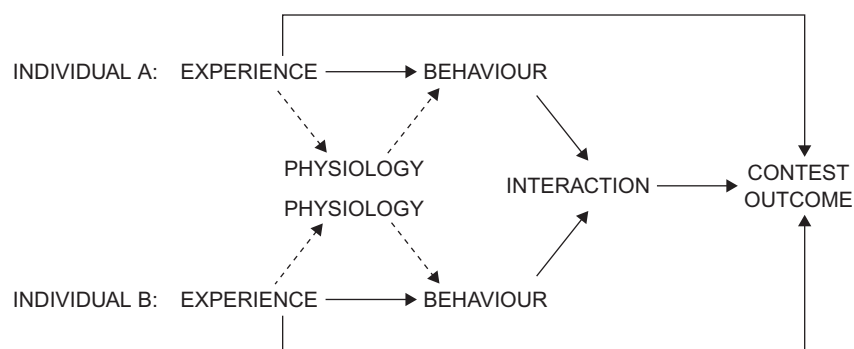
### 6.1 Introduction

Aggressive interactions are a common means of contesting resources for most animals. Considerable variation occurs in whether a specific individual wins a particular aggressive contest. Influences on the behaviour of individuals that might produce this variation include, among many factors, hunger, size, residency and age (Beaugrand *et al.* 1996; Hsu *et al.* 2005). Behavioural ecologists have been quite successful in understanding variation in contest outcomes, employing benefit/cost models to predict such things as contest duration and winner (e.g. Riechert 1998). Benefits are immediate or longer-term positive effects on fitness of the individual, such as gaining access to food or mates as a result of the contest. Costs include time and energy spent in the contest as well as the possibility of being injured or the increased chance of being taken by a predator.

Among fishes and a few other animals, including some insects, experience in a prior contest has been shown to influence the outcome of a later contest (Hsu *et al.* 2005). A recent winning experience tends to increase the chances of winning the current contest, while a losing experience tends to decrease the chance of winning. Among species tested so far considerable variation occurs in how much of an effect prior winning or losing experiences produce and how long the effect lasts. For most organisms winning and losing effects may last for different lengths of time and tend to be asymmetrical, with losing tending to have more influence than winning. Recent experiments indicate, as well, that multiple prior contests, rather than just the most recent experience, can affect behaviour during, and outcome of, the current contest (Hsu & Wolf 2001).

Most of the evidence from fish contests strongly suggests that the effects of prior contest experience influence the individual's perception of its own fighting ability and the accumulation of costs in a subsequent contest (Hsu *et al.* 2005). In contrast to many standard studies of experience effects on learning and memory, the examination of these effects on aggression are complicated by the necessity to consider more than one individual's experience in understanding contest outcomes. It is most likely the combined experience effects of the contestants that influence outcomes. How these combined effects are integrated into the ongoing behaviour of the contesting individuals is still very uncertain.

The effect of prior contest experience wanes over time and has the hallmarks of memory and forgetting. Following the definition of learning offered by Alcock (1993,



**Fig. 6.1** Pathways for individuals A and B from contest experiences to modified contest outcomes based on those experiences. The dashed lines represent internal (i.e. physiological) changes that influence behaviour. The solid lines represent external events, including behaviour, a subsequent interaction, and the outcome of that interaction that are affected by the experience. (Reproduced from Hsu *et al.* 2005, with permission.)

p. 29), ‘the durable modification of behaviour in response to information acquired from specific experiences’, one could argue that these experience effects reflect learning of the potential costs associated with aggressive interactions. Learning in a contest situation does occur in fishes. Classical conditioning can be used to train fishes to cues that signal an impending contest before the opponent is present (Hollis *et al.* 1995). However, if we also consider the mechanisms of learning – modification of neural pathways to facilitate particular behavioural patterns – then whether contest experience actually leads to learning is at present unknown. We will review some of the physiological changes that accompany the experiences, but cannot conclude at present whether learning is involved. Hence, this chapter will refer to experience effects in order not to appear to draw a firm conclusion about whether they actually constitute learning.

Physiological and behavioural modifications are intermediate stages in the translation of experiences into changed contest outcomes (Fig. 6.1). Examining experience effects on aggressive behaviour thus provides a way to investigate how physiological effects are reflected in behavioural variation of each contestant, which can, in turn, affect contest outcomes. These experience effects also influence social behaviour of organisms in as far as it is mediated by aggression. Specifically, contest experience and its effects on subsequent contests might be an important component of dominance hierarchy formation in group-living organisms, with or without individual recognition.

This chapter will review our current knowledge of how experience in contests influences physiology and behaviour and ultimately the outcome of subsequent contests. We also will explore quantitative models of integrating multiple experiences and rates of disappearance of experience effects as well as experience-based algorithms for predicting contest outcomes. Much of this work has been undertaken with fishes as model organisms and adds yet more evidence of the complexity of experience effects in fish behaviour.



## 6.2 Winner and loser effects in fishes

Many fishes adjust their contest behaviour in accordance with the outcomes of their previous agonistic interactions (see Table 6.1 in Hsu *et al.* 2005), but the changes in fighting behaviour vary between studies. After winning experiences, individuals generally are more likely to initiate contests with more costly (in terms of energy and risk of injury) behaviour (i.e. attack rather than display), to retaliate and escalate contests when attacked, and to have increased probabilities of winning the contests. In contrast, individuals with recent losing experiences become less likely to initiate and participate in any agonistic interactions and more likely to retreat without escalating fights when attacked. In this section, we discuss the influence of methodology on detecting experience effects and the occurrence and variation in winner and loser effects.

### 6.2.1 Methodological concerns in detecting experience effects

In fishes, as in other taxa, loser effects appear to be more commonly detected than winner effects and the importance of experience effects varies among species (Hsu *et al.* 2005). However, caution is needed when interpreting these results because of variation in the experimental procedures employed to examine experience effects. Hsu *et al.* (2005) discussed four methodological concerns in testing experience effects that might have substantial impacts on the interpretation of available empirical results. The first concern is the protocol used to offer fighting experiences to focal individuals: self-selection or random-selection. In self-selection methods, the winner and the loser of a fight are treated as having a winning and a losing experience, respectively. This procedure could confound the effect of fighting experience with intrinsic fighting ability (Chase *et al.* 1994; Bégin *et al.* 1996). Bégin *et al.* (1996) concluded that a self-selected winner would have a 0.67 probability of having intrinsically higher fighting ability than its size-matched, naive opponent (0.83 if compared with self-selected losers), as opposed to a 0.5 probability as usually assumed and tested. In contrast, random selection procedures give predetermined winning or losing experiences to individuals chosen at random by pitting the focal individuals against smaller, habitual losers or larger, habitual winners, respectively. This method attempts to randomize intrinsic differences between contestants in order to focus solely on the effects of the experiences.

The second concern is the frequency and duration of experience training. Experience training can cause energy depletion, bodily injury and physical exhaustion, perhaps differentially affecting winners and losers. Naive opponents do not undergo experience training and are not subject to these effects. Prolonged experience training can temporarily compromise the physical condition of trained winners and losers and lower their probabilities of winning against naive opponents. Consequently, winner/loser effects may appear to be less/more pronounced than they really are. The third concern involves the time interval between the completion of experience training and the subsequent contest. A long time interval provides focal individuals with a chance to recover from the physical exhaustion/injury of experience training. However, because experience effects decay with time (Bakker *et al.* 1989; Chase *et al.* 1994; Hsu & Wolf 1999), the length of this interval will influence the likelihood of



detecting any experience effects and the magnitude of the effects detected. The fourth concern relates to isolation of focal individuals before experience training. The purpose of this isolation is to allow focal individuals sufficient time for the effects of their previous fight to disappear. Without sufficient isolation time, the experience effects measured could be influenced by uncontrolled earlier experiences. With isolation procedures, one must also consider the effects of isolation itself on agonistic behaviour (Gomez-Laplaza & Morgan 2000). Bearing in mind the importance of these methodological issues, we will discuss the trends of experience effects.

### 6.2.2 *Asymmetrical winner and loser effects*

In most species of fishes, a winner effect often is less pronounced and disappears faster than a loser effect (Hsu *et al.* 2005). One exception to this general trend is the mangrove killifish (*Rivulus marmoratus*, Cyprinodontidae), in which winning and losing experiences appear to have opposite but equal effects on contest outcomes (Hsu & Wolf 1999). No studies have explored the possible causes/mechanisms either for the observed asymmetries in winner and loser effects or the variation in the degree of the asymmetry. We will discuss here some hypotheses for the asymmetry, which can be tested in the future. One possible adaptive explanation for this often greater and longer-lasting loser effect is that engaging in contests but losing often incurs more costs (time, energy, injuries) than retreating without confrontation (Neat *et al.* 1998). These high costs of losing could select for individuals that adopt more 'conservative' strategies such that their fighting behaviour is more likely to be modified by losing experiences than by winning experiences. It will be interesting to test whether the cost of losing is correlated with the degree of asymmetry between winner and loser effects. Nonetheless, methodologies for quantifying costs and experience effects probably should first be standardized to facilitate such comparisons.

The asymmetrical winner and loser effects also could be a consequence of loser effects being more easily reflected in the probability of winning than winner effects (Mesterton-Gibbons 1999). Individuals with prior losing experience often voluntarily retreat from a subsequent contest without physically interacting with their naive opponents (e.g. Bakker & Sevenster 1983). Contests between prior winners and naive opponents are likely to escalate into physical fights (e.g. Hsu & Wolf 1999). Prior contest experiences are expected to influence an individual's perception of its own fighting ability and the costs of a future contest without altering the individual's true fighting ability (Hsu *et al.* 2005). In that case, once a contest escalates, the value of information from past fighting experience is greatly diminished and contest outcome should be determined primarily by the intrinsic fighting ability of the two contestants. Thus, with a higher proportion of escalations, the probability of prior winners defeating naive, size-matched opponents will be less likely to deviate from 0.5.

### 6.2.3 *Interspecific variation in experience effects*

The importance and permanence of experience effects vary among species (Hsu *et al.* 2005); for instance, immediately after experience training, the probability of prior winners winning against size-matched, naive opponents ranges from 0.5 [no effect; e.g. paradise fish, *Macropodus opercularis* (Anabantidae); Francis 1983] to



0.78 [pumpkinseed sunfish, *Lepomis gibbosus* (Centrarchidae); Chase *et al.* 1994] in different species. And, winner effects could decay completely within an hour or last more than 2 days (mangrove killifish, Hsu & Wolf 1999). Loser effects are just as variable among species; the probability of prior losers winning against size-matched naive opponents varies from 0.5 [green swordtail fish, *Xiphophorus hellerii* (Poeciliidae); Earley & Dugatkin 2002] to 0.0 [sticklebacks, *Gasterosteus aculeatus* (Gasterosteidae); Bakker *et al.* 1989] and the effect could disappear within 24 h (as suggested by non-analysed preliminary data, Bakker *et al.* 1989) or last more than 3 days (paradise fish; Francis 1983). Part of this variation may be explained by differences in the duration of experience training among different studies. Sticklebacks were trained only for 15 min and their loser effects disappeared fastest (within less than 24 h; Bakker *et al.* 1989); mangrove killifish were trained for an hour and their loser effects were already limited 2 days after experience (Hsu & Wolf 1999); paradise fish were trained for 24 h and their loser effects lasted considerably longer (still significant 3 days later; Francis 1983). This pattern could arise from the duration of experience training influencing the magnitude and/or decay rate of experience effects. The frequency of social encounters also might influence how long information from a social interaction is retained (Schuett 1997; Hsu *et al.* 2005). If, as expected, outcomes of past contests provide individuals with information regarding the costs of engaging in aggressive interactions, individuals in populations with a higher frequency of social encounters will obtain recent and more reliable information more often. Thus, these individuals should preserve information from past interactions to a lesser extent than individuals in populations with a low frequency of social encounters.

#### **6.2.4 Importance of experience effects in fighting decisions and outcomes**

Although past experience has an important impact on fighting decisions, it is only one of the many factors that influence estimated benefits and/or costs for the contestants. Past experience presumably provides individuals with information regarding the costs of engaging in contests in a similar way to other characteristics related to fighting ability (e.g. size, weaponry). The value and reliability of these indicators of fighting ability increase as asymmetries between contestants increase. Also, as the reliability and importance of other cues increases, the usefulness of prior experience might decrease; for instance, the importance of experience effects on contest outcome is negatively influenced by body size asymmetry (e.g. pumpkinseed sunfish, Beacham 1988; green swordtail fish, Beaugrand *et al.* 1991, 1996). Asymmetries in resource value, prior residency (Beaugrand *et al.* 1996), energy reserves (Marden & Waage 1990), and other factors that influence contest costs (e.g. predation) also should have an impact on the importance of experience effects and should be considered when investigating experience effects on fighting strategies.

#### **6.2.5 Experience and dominance hierarchies**

The majority of empirical research on experience effects and contest behaviour has been conducted in dyadic contests (but see Chase *et al.* 2003; Dugatkin & Druen



2004). This dyadic method is critical for determining some of the more intricate aspects of experience effects (e.g. decay rates, symmetry, etc.) but essentially removes individuals of many species from their natural social context. Social organisms often are found in groups that interact in ways that range from loosely defined dominance structures to rigid linear hierarchies. These patterns of structural group organization exist for varying periods of time depending usually on the breeding season of the population. Is it possible that changes in individual perceptions of benefits and/or costs via consecutive wins or losses impact the form and/or structure of dominance hierarchies? Early notions held that intrinsic differences between group members in individual attributes such as size were paramount in determining an individual's place in the hierarchy (Collias 1943; Allee *et al.* 1955). Currently, some empirical evidence and a burgeoning theoretical literature indicate that experience effects can predict a much of the variation in the observed patterns of dominance-hierarchy formation. Empirical evidence for the role of experience effects in dominance-hierarchy formation is slim and stems primarily from tests of Chase's (1980) 'jigsaw model', which posited that linear dominance hierarchies in small groups can emerge from patterns of consecutive wins (double dominance) or losses (double subordination) among group members. These patterns, and subsequent linear hierarchy formation, have been observed in primates (Barchas & Mendoza 1984), birds (Chase & Rohwer 1987), fishes (Chase *et al.* 2002) and invertebrates (Goessmann *et al.* 2000). Evidence also indicates that subjecting one animal to a win or loss can alter its place in a dominance hierarchy (Alexander 1961; Nelissen & Andries 1988). Perhaps the most convincing empirical support for experience effects mediating hierarchy formation comes from a study on swordtail fish (Dugatkin & Druen 2004). Using a random selection procedure, size-matched swordtail males were given winning, losing, or no experience and were then placed together to form a dominance hierarchy. Hierarchies in which previous winners achieved the dominant rank, inexperienced animals the middle rank, and prior losers the lowest rank were significantly more frequent than expected by chance.

Theoretical models provide, at present, the most useful framework for investigating changes in hierarchy structure that result from manipulating factors associated with experience effects. Hsu *et al.* (2006) provide a detailed description of how properties associated with translating experience effects into contest outcomes might affect hierarchy structure. These properties include which decision rules are employed, the symmetry, magnitude and decay of experience effects, how the effects accumulate, and the limits to changes in perceived fighting ability. No consensus exists as to how these properties affect hierarchy structure, either individually or in tandem. This is true even for properties that are commonly manipulated in experiments and simulation models, such as symmetry; for instance, although symmetrical experience effects (equal magnitude, opposite sign) are sufficient to generate a linear hierarchy among a set of initially identical individuals (Bonabeau *et al.* 1999; Hemelrijk 2000; Beacham 2003), it is unclear how hierarchy linearity responds to deviations from symmetry (see Bonabeau *et al.* 1996 and Dugatkin 1997 for opposing predictions). No simulation models to date have systematically explored the influence of different modes of accumulation of experience effects (additive versus multiplicative; see section 6.5, equations 6.1 and 6.2) or limits to increases in perceived fighting ability (i.e. bounds) on emergent hierarchy structure, and very few have



manipulated decision rules, interaction frequencies, or decay functions (Bonabeau *et al.* 1996; Hemelrijk 1999; Beacham 2003). It might be difficult to maintain the tractability of simulation models while altering simultaneously all of these properties and introducing variation in intrinsic fighting abilities. However, attempts to do so could provide new insights into the complex influences of experience effects and how and to what degree experience effects shape dominance hierarchies. These modelling approaches should also focus future empirical research.

### 6.3 Mechanisms of experience effects

Behavioural changes that result from modifications in an individual's perception of costs during and/or after an aggressive contest are likely to be mediated by two somewhat different but overlapping neuroendocrine mechanisms. Changes in neural circuitry facilitate the consolidation and retrieval of information related to contest costs and these types of learning processes are, in turn, influenced to some degree by neuroendocrine factors such as hormone concentrations (e.g. glucocorticoids; Roozendaal 2002). Similarly, integration of information and associated changes in neural circuitry can elicit neuroendocrine changes that allow an animal to respond appropriately to perceived alterations in contest costs. A brief overview of studies that link learning with fighting experience follows below, and it discusses some of the most salient neuroendocrine changes that occur as a result of winning or losing aggressive encounters, keeping in mind that learning itself is a manifestation of changes in neuroendocrine systems.

#### 6.3.1 Learning

Psychology has a long history of research into how experiences promote learning of the expectations of benefits and costs of alternative possible behaviours. Pigeons can adjust the frequency of pecking at keys in relation to differential food rewards and gradually improve their performance with repeated trials (Mazur 1995). These changes can be stored in long-term memory for retrieval and used in key-pecking choices at later times. Many memory traces also gradually disappear (forgetting) through time, whether spontaneously or as a result of interference from more recent experiences (Mazur 1996; Devenport 1998).

Recently, more emphasis has been placed on understanding how conditioning, particularly Pavlovian conditioning, might mediate social behaviour (Domjan *et al.* 2000). A series of studies on blue gouramis (*Trichogaster trichopterus*, Osphronemidae) showed that learning to anticipate a rival could reduce the costs of fighting and increase an individual's chances of winning the potential fight through early engagement of the intruder (Hollis 1984, 1999; Hollis *et al.* 1995). Individuals conditioned to anticipate the appearance of a rival, through pairing of a light stimulus with presentation of a rival, were more successful at expelling the intruder from their territory than individuals that had not been conditioned. Success in this initial contest also influenced the probability of winning a future contest (Hollis *et al.* 1995). Similar effects have been demonstrated in three-spined sticklebacks (*Gasterosteus aculeatus*; Jenkins & Rowland, 1996).



Although these studies provide evidence that learning can modulate aggressive behaviour in fishes, identifying the mechanism of learning, if any, that characterizes winner and loser effects presents a considerable challenge. So-called conditioned defeat, which is similar to the loser effect, has been studied extensively in rodents (Huhman *et al.* 2003) but the type of conditioning underlying these effects remains elusive. Changes in behaviour of winners and losers emerge without explicit pairing of conditioned and unconditioned stimuli, thus Pavlovian conditioning is unlikely to be involved. Both winners and losers receive some form of reinforcement, whether positive or negative, and subsequently respond with increases or decreases in aggressive behaviour when presented with a different opponent. These types of behavioural changes appear, superficially, to be the result of operant conditioning but because individuals respond in a more general fashion to similar stimuli (e.g. conspecific opponents), one might qualify the behavioural responses of winner and loser as sensitization (in losers) or stimulus generalization. To establish empirically that experience effects constitute learning might require a reformulation or combination of learning rules coupled with a better understanding of how extinction, forgetting rates, and spontaneous recovery might contribute to intraspecific and interspecific variation in the expression of winner and loser effects. It also will be important to establish whether changes in the behaviour of winners and losers occur as a consequence of, for instance, hormones acting on already established neural pathways or the emergence of new neural pathways that facilitate appropriate behavioural responses in the long term. The experience of both opponents influences the dynamics and outcome of an aggressive contest. Thus, approaching experience effects from a learning perspective will require consideration of learning processes that occur after an initial experience and during the current contest for both contestants (Miklósi *et al.* 1997).

### 6.3.2 Neuroendocrine correlates of fighting

A thorough review of the literature documenting manifold neuroendocrine changes that accompany fighting experience is beyond the scope of this chapter. It will touch briefly on four approaches to studying physiological changes associated with winning or losing aggressive interactions.

The first approach entails measurement of, for instance, hormone or brain neurotransmitter concentrations following contest resolution. In fishes, losers often exhibit increased cortisol concentrations (Hoglund *et al.* 2001; Sloman *et al.* 2001), decreased androgen levels (Cardwell & Liley 1991; Oliveira *et al.* 1996), and increased serotonergic [5-hydroxytryptamine (5-HT)] activity (Winberg & Nilsson 1993) compared to winners. Relative hormonal responses of winners and losers, however, may vary considerably. In some studies, no substantial differences between winners and losers in post-fight cortisol concentrations are found (Correa *et al.* 2003; Buchner *et al.* 2004; R.L. Earley, J.T. Edwards, O. Aseem, K. Felton, L.S. Blumer, M. Karom & M.S. Grober, unpublished observations), and a direct association between winning and elevated androgen levels rarely is observed (e.g. Neat *et al.* 1998; Elofsson *et al.* 2000). An important factor that might explain variation in documented responses across studies is the dynamics of the aggressive contest. The neuroendocrine response of both winners and losers appears to be linked to



the intensity and/or length of the contest (e.g. number of escalated interactions or degree of aggressive reinforcement; Winberg & Lepage 1998; Elofsson *et al.* 2000; Sloman *et al.* 2001). Another important factor to consider is the strength of the neuroendocrine response. In particular, hormones associated with the stress response (e.g. cortisol and norepinephrine) will enhance aggression when secreted in low concentrations, but beyond a certain threshold these same hormones will inhibit aggressive behaviour (Haller *et al.* 1998; Øverli *et al.* 2002). Recent evidence also suggests that hormonal responses to fighting, particularly elevations in androgen levels, may be linked to perceptions of contest success rather than the act of fighting alone (Oliveira *et al.* 2005).

The second approach examines changes in the neuroendocrine response of winners and losers over time. This approach is important for understanding the potential for neuroendocrine factors to mediate the differential longevity of winner and loser effects (Hannes *et al.* 1984; Winberg & Lepage 1998; Øverli *et al.* 1999; Summers *et al.* 2003) discussed in Section 6.2.2. Both cortisol concentrations and 5-HT metabolism increase sharply following a contest in both winners and losers, but winners recover baseline concentrations/metabolism much faster than losers. It is tempting to link post-fight temporal decay of plasma hormone or brain neurotransmitter concentrations directly with the persistence of winner and loser effects. However, explicit causal relationships between temporal decay of neuroendocrine factors and similar decay in experience effects have yet to be established.

The third approach involves manipulating hormones, transmitters, or receptor binding capabilities and documenting changes in the expression of behaviour associated with fighting experience. The most common manipulation in fishes is to alter baseline levels of hormone or neurotransmitter via implantation or injection; for instance, androgen supplementation and injections of serotonin synthesis inhibitors facilitate aggressive behaviour in cichlid fishes (Fernald 1976; Adams *et al.* 1996). Beyond this, we know very little about how exogenous manipulations affect the fighting behaviour of fishes. This is due, in part, to the methodological difficulties of conducting such treatments in an aqueous medium on relatively small organisms (which are typically the focus of experimental studies on aggression). Studies on rodents and birds however, have demonstrated that a variety of neuroendocrine factors can affect aggressive behaviour if applied exogenously (e.g. serotonin reuptake inhibitor, Larson & Summers 2001; androgens, Trainor *et al.* 2004; arginine vasotocin, Goodson 1998). Importantly, some studies in laboratory rodents have successfully regulated the acquisition and/or expression of behaviour associated with defeat by infusing different types of receptor agonists/antagonists into the brain (e.g.  $\alpha$ -amino butyric acid and corticotropin releasing hormone receptors; Jasnow *et al.* 1999; Jasnow & Huhman 2001). These studies provide some compelling directions for exploring the neuroendocrine correlates of the loser effect in fishes.

Lastly, it is important to recognize that aspects of the peripheral and central neuroendocrine systems do not act independently on aggressive behaviour. Changes in aggressive behaviour as a consequence of winning or losing a contest are likely to result from complex interactions between, and correlated changes among hormones, neuropeptides, neurotransmitters, and their receptors (e.g. interactions between the serotonergic system and the neuroendocrine stress axis; Winberg *et al.* 1997). Furthermore, behavioural outcome may depend critically on the site at which



neuroendocrine interactions take place (e.g. hypothalamus, forebrain preoptic area; Hayden-Hixson & Ferris 1991; Kruk *et al.* 2004).

## 6.4 Other types of experience

### 6.4.1 Individual recognition

The behavioural decisions of shoaling fishes (Griffiths 2003) and the dynamics of competitive interactions in territorial species (Miklósi *et al.* 1995; Miklósi *et al.* 1997) are mediated, in part, by the ability of individuals to distinguish familiar conspecifics (see Chapter 8). Individual recognition can reduce fighting costs in situations where the probability of encountering the same individual on a regular basis is high (Pagel & Dawkins 1997). In fishes, memory of past opponents is ascertained by comparing the behavioural response of losers when encountering their former dominant opponent and an unfamiliar opponent. Generally speaking, losers exhibit more pronounced behavioural and physiological (e.g. skin darkening) avoidance responses when faced with familiar opponents (Miklósi *et al.* 1995, 1997; Morris *et al.* 1995; Johnsson 1997; O'Connor *et al.* 2000; Utne-Palm & Hart 2000), suggesting that individual recognition amplifies the loser effect. Contests between familiar opponents seldom escalate and typically are characterized by low levels of aggression (Keeley & Grant 1993; Earley *et al.* 2003). It is thus unclear whether winners fail to escalate because they recognize a former subordinate and/or because the opponent behaves submissively.

### 6.4.2 Eavesdropping

In some fish species, individuals appear to obtain a relatively accurate estimate of possible costs in future contests by watching others engage in aggressive contests. Eavesdropping, the act of extracting information from contest interactions between others (Peake & McGregor 2004; Peake 2005), might be a particularly advantageous assessment strategy when the costs of physical combat are high (Johnstone 2001). In Siamese fighting fish (*Betta splendens*, Osphronemidae) and green swordtail fish, observers appear to update their perception of the fighting abilities of the watched individuals based on the dynamics and/or outcome of the witnessed contest (Oliveira *et al.* 1998; McGregor *et al.* 2001; Earley & Dugatkin 2002; Brown & Laland 2003).

An important consideration for studies on eavesdropping in fishes is whether the observer's response is specific to the watched individuals or more general. Observing an aggressive interaction elevates urinary 11-ketotestosterone levels [Mozambique tilapia, *Oreochromis mossambicus*, (Cichlidae); Oliveira *et al.* 2001] and increases the aggressive behaviour of male Siamese fighting fish towards unobserved opponents. It is possible that watching fights elicits behavioural and physiological 'priming' responses (Hollis *et al.* 1995), which cause postobservational changes in agonistic behaviour, independent of integrating information about the observed contestants. Studies on green swordtail fish, however, indicate that eavesdroppers modify predictably their response towards individuals that had been observed to win or lose,





but not towards naive animals (Earley & Dugatkin 2002; Earley *et al.* 2005). These results suggest that at least some species are capable of storing information from watched contests for use in future encounters with the observed individuals.

Recent simulation models have addressed whether eavesdropping can act in concert with winner and loser effects to promote linear dominance hierarchies (Dugatkin 2001). Resulting in part from unnecessarily strict assumptions (Earley & Dugatkin 2005), the verdict is uncertain but there is some indication that indirect experience, and subsequent adjustments of perceived relative fighting ability by an eavesdropper, reinforces linear hierarchies (Dugatkin 2001).

### 6.4.3 *Transitive inference*

Transitive inference in a social context refers to the ability of an individual to combine individual experience with a particular opponent and information obtained through eavesdropping. Fusing these two types of experiences allows an animal to respond more appropriately to its social environment; for instance, if individual A initially loses to B and then witnesses C defeat B, A may also opt not to interact with C so as to avoid the costs of fighting and losing again. Altmann (1981) proposed that non-primate animals were incapable of transitive inference, but pinyon jays (*Gymnorhinus cyanocephalus*; Paz-y-Miño *et al.* 2004), chickens (*Gallus gallus*; Hogue *et al.* 1996), and hyenas (*Crocuta crocuta*; Engh *et al.* 2005) show the capacity for transitive inference, or at least assessment of third-party relationships, in a social context (see also Peake *et al.* 2002 for support in great tits). Combining individual recognition with eavesdropping may reduce errors in assessment of fighting ability and, in turn, further reduce rank-order ambiguity in dominance hierarchies (e.g. Hogue *et al.* 1996; Peake *et al.* 2002). Despite the fact that fishes are well represented in studies on individual recognition and eavesdropping, researchers have yet to test whether species within this taxon are capable of transitive inference. This marks an exciting direction for research on fish cognition over the next decade.

## 6.5 Integrating experience information

The information derived from previous fighting experience is expected to modify perceptions of fighting costs for individuals in future contests, influence their interactions, and ultimately impact contest outcomes. To understand and model the influence of prior fighting experiences on contest outcomes, we need to consider at least five components:

- 1 pre-experience expectations;
- 2 the effect of an experience;
- 3 how that effect changes with time after the experience;
- 4 how multiple experiences are integrated for an individual;
- 5 how the experiences of two individuals interact to determine their probabilities of winning against each other.

Socially naive individuals are aggressive and engage in contests when encountering conspecifics for the first time (Doernberg *et al.* 2001; Chen *et al.* 2002); for



instance, socially naive fishes are capable of defeating their competitors to acquire winning experiences (e.g. stickleback, Bakker & Sevenster 1983; mangrove killifish, Hsu & Wolf 1999). These naive individuals are likely have intrinsic estimates of their own fighting abilities and the possible costs of engaging in contests. Experiences then modify perceived contest costs from what would be expected by naive individuals.

Individuals are likely to participate in more than one aggressive encounter and thus need to process information from these multiple events. Empirical data on the effects of multiple fighting experiences are limited. The contest behaviour of the mangrove killifish is influenced at least by the most recent and the penultimate fighting experiences (Hsu & Wolf 1999, 2001), indicating that the fishes can integrate information from different experiences. The mangrove killifish probably is not the only fish species that uses information from multiple contest experiences. Two mechanisms of experience accumulation often have been considered in the literature on dominance hierarchy formation, additive (e.g. Bonabeau *et al.* 1999; Hemelrijk 2000; Beacham 2003) and multiplicative (e.g. Dugatkin 1997). To allow different experiences to have different magnitudes of effects and decay rates, Hsu *et al.* (2006) proposed a general model for additive effects:

$$F_i = N_i + \sum_{I=1}^a (E_I \times W_{I,t}) \quad (6.1)$$

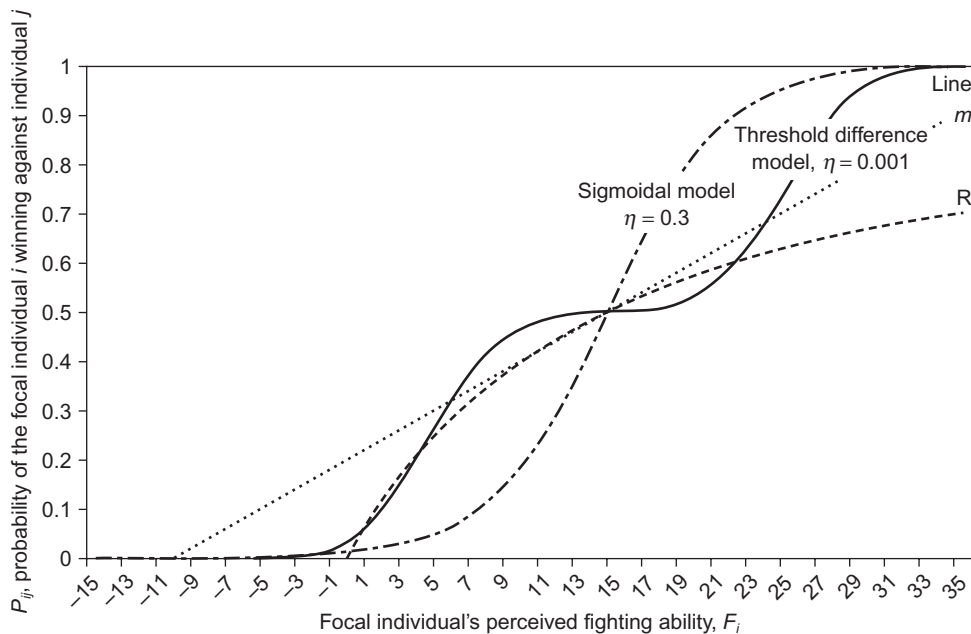
where  $F_i$  is individual  $i$ 's perceived fighting ability (reflected in perceived costs) after  $a$  fighting experiences;  $N_i$  is the perceived fighting ability of individual  $i$  in the naive state;  $E_I$  is the information individual  $i$  received and incorporated from experience  $I$ ; and  $W_{I,t}$  represents how the effect of experience is weighted with the passage of time or the occurrence of additional experiences. The sign of  $E_I$  is positive for a win and negative for a loss. Equation 6.1 can be modified for multiplicative effects:

$$F_i = N_i \times \prod_{I=1}^a (1 + E_I \times W_{I,t}) \quad (6.2)$$

These two mechanisms of information integration differ in the relationship between experience effect and perceived fighting ability. In the additive model, the experience effect is  $E_I$  and is independent of the naive individual's perceived fighting ability  $N_i$ . In the multiplicative model, the experience effect,  $N_i * E_I$ , depends on the individual's perceived fighting ability and individuals with higher perceived fighting ability are subjected to stronger experience effects. Consequently, successive winning experiences will result in a more pronounced change in the perceived fighting ability than successive losing experiences. Although the magnitude of an experience effect may be influenced by the state of an individual, the relationship between experience effect and perceived fighting ability has not yet been examined.

If experience effects decay slowly and the frequency of fighting is high, it is theoretically possible that  $F_i$  could become large or become negative. However, physiological mechanisms that mediate experience effects may impose a limit (minimum/maximum) on the effects; for instance, hormone titres presumably cannot increase indefinitely. However, what regulates the ceilings of experience effects is





**Fig. 6.2** Probability of winning ( $P_{ij}$ ) predicted from: the Linear model [Eqn 6.3, with  $m$  arbitrarily set to 0.02]; the Relative model [Eqn 6.4]; the Sigmoidal model [Eqn 6.5, with  $\eta$  arbitrarily set to 0.3]; and the Threshold difference model [Eqn 6.6, with  $k$  set to 3 and  $\eta$  arbitrarily set to 0.001] for a focal individual  $i$ . Curves plotted as perceived fighting ability ( $F_i$ ) of the focal individual  $i$ , fighting against an opponent  $j$  with a perceived fighting ability ( $F_j$ ) of 15. (Modified from Hsu *et al.* 2005.)

currently unknown. Different limits could be imposed to allow  $F_i$  to vary within a biologically meaningful range of values for different groups/species of animals.

Contest outcomes result from interactions between rivals. Hsu *et al.* (2005) proposed four models that predict fighting outcomes based on the experience-modified perceived fighting abilities of two opponents (Fig. 6.2).

Model 1 is a Linear model:

$$P_{ij} = 0.5 + m(F_i - F_j) \quad (0 \leq P_{ij} \leq 1), \quad (6.3)$$

where  $P_{ij}$  is the probability of individual  $i$  winning against individual  $j$ . The slope,  $m$ , scales how important differences in the experience-modified perceived fighting abilities are to contest outcome. In this model, the probability of winning is a linear function only of the difference in the perceived fighting abilities of the opponents.

Model 2, the Relative model:

$$P_{ij} = \frac{F_i}{F_i + F_j} \quad (0 \leq P_{ij} \leq 1). \quad (6.4)$$

In this model, the probability of winning is determined by the relative ratio of the perceived fighting ability of the two opponents. Consequently, the influence



of experience is negatively scaled by the sum of the perceived fighting ability of the two opponents. Experience effects are more difficult to detect between bigger contestants or contestants with more winning experiences.

Model 3, the Sigmoidal model (following Bonabeau *et al.* 1999):

$$P_{ij} = \frac{1}{1 + e^{-\eta(F_i - F_j)}} \quad (6.5)$$

where  $\eta$  scales the rate of approach to the asymptote. A large  $\eta$  produces a deterministic outcome and a small difference in the experience-modified perceived fighting ability would be sufficient to ensure winning by the opponent with a slightly higher perceived fighting ability.

Model 4, the Threshold Difference model:

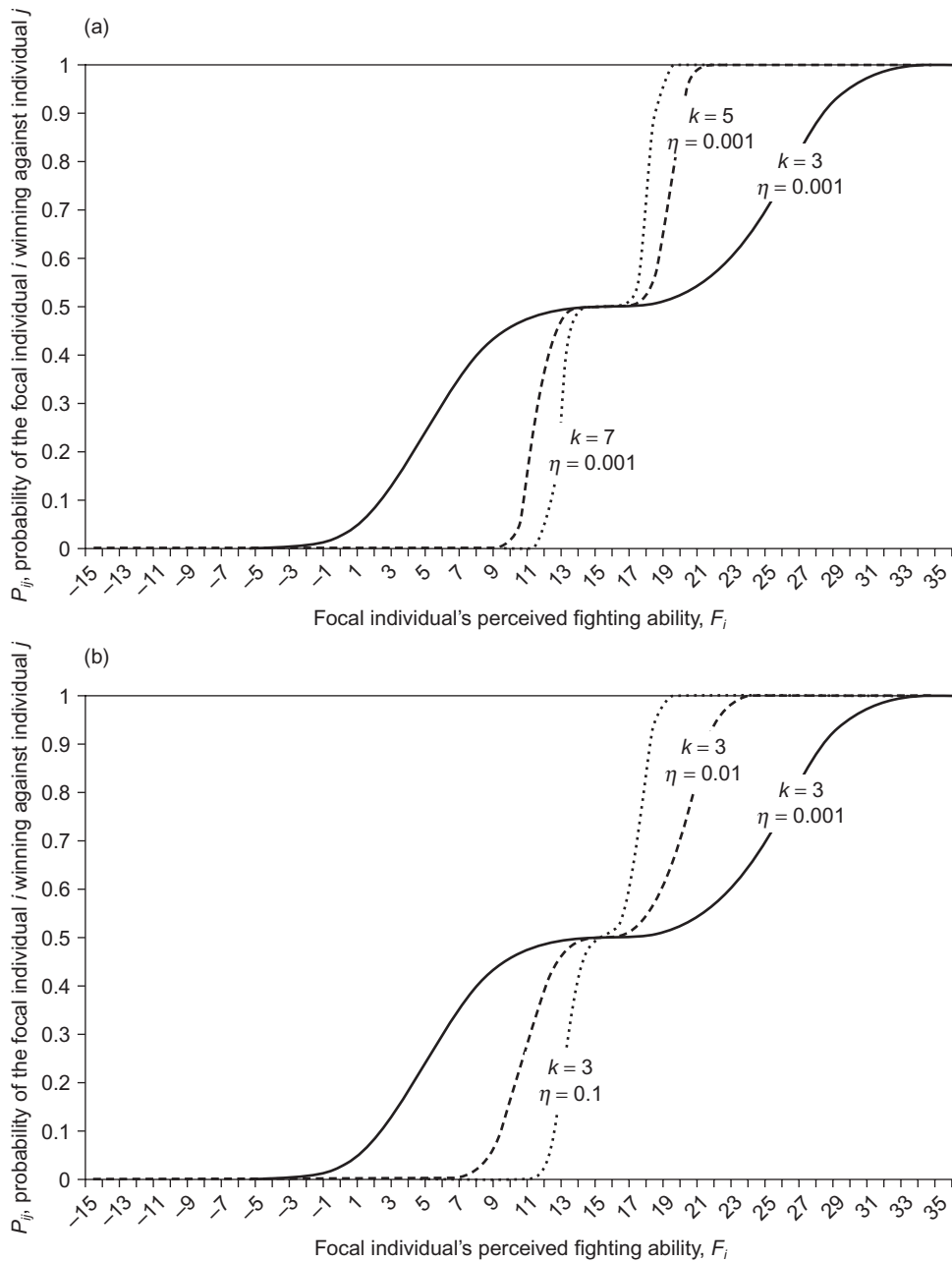
$$P_{ij} = \frac{1}{1 + e^{-\eta(F_i - F_j)^k}} \quad (6.6)$$

where  $k$  could be any odd number  $\geq 3$ . In this model, small differences in the perceived fighting abilities do not produce detectable effects on fighting outcomes. But once the differences become sufficiently large (i.e. beyond a threshold) then changes occur rapidly toward the asymptote. The parameters  $\eta$  and  $k$  influence both: (i) the width of the interval where fighting outcome remains insensitive to the difference in perceived fighting ability; and (ii) how fast the probability of winning approaches the asymptote once the difference reaches the threshold. With a small  $\eta$  and/or  $k$ , a big difference in perceived fighting ability is needed to produce a recognizable effect on the contest outcome and the probability of winning approaches the asymptote at a slower rate. However, a change in  $\eta$  produces a bigger impact on how fast the difference reaches the threshold, while a change in  $k$  produces a bigger influence on how fast the probability of winning approaches the asymptote once the difference reaches the threshold (Fig. 6.3a,b).

The Linear and the Relative models theoretically could yield  $P_{ij} < 0$  or  $> 1$ , which are empirical impossibilities. However, the theoretical possibility means that even with temporal decay of experience effects,  $P_{ij}$  could remain at 0 or 1 for some period of time until the combined experience effects decay to values that yield  $P_{ij}$  between 0 and 1.  $P_{ij}$  is bounded between 0 and 1 in the Sigmoidal and the Threshold Difference models.

These models make different predictions regarding the relative importance of wins and losses on contest outcomes, even if wins and losses have equivalent effects on an individual's perceived fighting ability. Models 1, 3, and 4 predict that, once integrated, wins and losses have the same magnitude of effects on the probability of winning while the Relative model predicts a more prominent loser than winner effect on contest outcomes. This predicted outcome asymmetry from the Relative model could partially explain why losses have more effect than wins in many contests (see Section 6.2.2) and may explain why the influence of winning or losing may disappear/decay at varying time intervals/rates (Francis 1983; Bakker *et al.* 1989; Chase *et al.* 1994). Empirical data are necessary to understand the applicability of the four models.





**Fig. 6.3** A comparison of the influences of parameters  $k$  and  $\eta$  on the predictions from the Threshold difference model [Eqn 6.6]. (a) The impact of parameter  $k$  (with  $\eta$  fixed at 0.001 and  $k$  set to different values (3, 5 and 7, respectively)). As  $k$  increases, the function approaches asymptote much faster. Although the interval where the probability of winning ( $P_{ij}$ ) remains relatively insensitive to the difference in perceived fighting ability, ( $F_i - F_j$ ) becomes narrower as  $k$  becomes bigger, the interval does not disappear as fast as when  $\eta$  changes [as in (b)]. The impact of parameter  $\eta$  [with  $k$  fixed at 3 and  $\eta$  set to different values (0.001, 0.01 and 0.1, respectively)]. As  $\eta$  becomes bigger, the function also approaches the asymptote faster; and, relative to the curves in (a), the insensitive interval becomes narrower faster.



## 6.6 Conclusions and future directions

The evidence for fishes and other animals strongly supports an effect of prior contest experience on physiology and behaviour and hence on the outcome of a current contest. These effects vary in their magnitude and with the longevity of earlier winning and losing experiences, and appear to be based on changed perceptions of fighting ability and the costs of the current contest. These changed perceptions can be viewed as at least similar to the phenomena of learning and forgetting of cost expectations based on accumulated experiences.

While we know that these experience effects on aggression occur, we know very little about the details of the effects. We have discussed hormonal changes following contest interactions. Generally one finds considerable variation in hormonal responses but often testosterone is elevated following a win and corticosteroids are elevated following a loss. At the same time, behaviour changes so that winners tend to be more aggressive, willing to initiate a subsequent contest and more willing to attack an opponent, while losers tend to be less likely to participate in a contest. In spite of considerable work in this area, we still know relatively little about the detailed relationships between an experience and its effects on physiology, behaviour and contest outcome. Currently, most studies focus on only one or two stages of the process that transforms experiences into changed contest outcomes (Fig. 6.1). Integrating all stages will be complicated, but ultimately most productive in understanding how experience influences aggression.

Complicating interpretation of changes produced by experiences is the fact that contest outcome is probably based on the relationship of the effects on each contestant, not merely the magnitude of the effects on a single individual. The importance of the interaction in contest outcome requires that models making quantitative predictions of contest outcome include the magnitude of experience effects at any time and how those experience effects of the contestants are integrated to determine contest outcome.

Models integrating multiple experiences assume the effects are additive or multiplicative, but with little supporting evidence. So far experiments have tested a maximum of two prior experiences with only a single interval length between experiences and the subsequent contest. The rate of decay of the effects of individual experiences also is unknown. However, it is clear that the decay rate varies among species and even some populations (e.g. sticklebacks; Mackney & Hughes 1995). Predictions about contest outcomes based on prior experience of the contestants will depend on careful documentation of the symmetry and magnitudes of initial effects and their subsequent decay rates as well as the mode of accumulation of multiple experience effects.

This chapter summarises four different algorithms for predicting contest outcomes from differences in integrated experience effects (Hsu *et al.* 2005). The algorithms differ in the importance of small differences in experiences between the contestants and the degree to which the predicted outcome asymptotes as differences in experience effects become large. The only study of which we are aware that attempts to test predictive power of the algorithms has looked at Equations 6.1 and 6.2. These two models each give good fits to the data on contest outcomes with similar values for additive experience effects at 24 and 48 h following the experiences (Y. Hsu,



unpublished data). Carefully designed tests will be required within time limits where experience effects are predicted to be most dissimilar to distinguish among the four current algorithms for their predictive power. One difficulty of this approach is that we do not have estimates of the values of wins and losses at various time periods that are independent of the outcomes data. It will be useful to develop ways to gain independent estimates of these effects.

These algorithms for integrating multiple experience effects and predicting contest outcomes are important for predictions about the role of experience in dominance hierarchy formation. Various models have used additive or multiplicative integration of multiple experiences and have assumed the form of the algorithm predicting contest outcomes. Moving from qualitative to quantitative predictions of contest outcome and hierarchy formation, based on interaction frequencies and experience decay rates, will be an important component of testing recent theoretical models of hierarchy formation.

The experience effects for an individual need not be obtained by direct participation in a contest. Evidence now indicates that observing other individuals fighting can influence future interactions with either fighter, in this case presumably based on the expectation of the costs that could be imposed by the observed fighter. This eavesdropping implies memory of the identity of the individuals and their activities in the fight. Some evidence also suggests that observing a contest can modify the observer's behaviour in subsequent contests (Clotfelter & Paolino 2003). In this case, the bias in behaviour produced by the earlier observations would be with any contestant, not just the ones in the previous contest. This possibility is more problematic and awaits further experimental testing.

Our potential ability to manipulate physiology and behaviour by prior experience also should give us a useful tool for understanding how these two phenomena influence contest outcome. Using experience as an experimental tool to investigate signalling in aggressive interactions also should help us understand the role of self-perception and relative comparisons to the opponent in outcomes of contests. Most game theoretical models assume some comparison to the opponent, but it is possible that self-perception is critical for behaviour in a contest.

Considerable progress has been made in understanding how experience influences subsequent contest behaviour and outcomes, but all aspects of the phenomenon need considerable more research before we approach a reasonable understanding of physiology, behaviour and contest outcomes. As that work moves forward we also need to integrate experience effects into other influences on contest outcomes. Size differences between individuals, residency and differences in perception of possible benefits from the aggression, among other possible factors, would all be expected to be integrated into outcomes of particular contests. Determining the relative importance of each factor has received little investigation and certainly warrants much more effort.

Fishes are very tractable experimental organisms for research on factors, including experience, that influence aggressive behaviour and contest outcomes. In fact, most of the work on this problem so far has been undertaken with fishes and we expect that they will probably increase in importance as model organisms for answering questions in this very fascinating area of behavioural research.



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