Chapter 6

Aggressive Behaviour in Fish: Integrating Information about Contest Costs

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6.1   Introduction

As the introductory chapter to the first edition of this book (Brown *et al*. 2006) noted, fish behaviour has long been viewed as stereotyped and not strongly influenced by context or experience. The recognition that experience and learning can influence fish behaviour coupled with observations of considerable variation in behaviour within and between individuals has led to an increasing awareness of the complexity of fish behaviour. Behavioural ecologists are interested in understanding the causes and effects of behavioural variation within individuals (e.g. over time), among individuals of a population and among populations. These causes and effects are related to the benefits and costs of the behaviour that influence the evolutionary success (fitness) of the individual.

Over 40 years ago Tinbergen (1963) noted that behavioural variation could be examined from multiple perspectives. This variation could result, for example, from differences within and among individuals in genetics, age, size, sex, developmental history and morphological and physiological constraints. The variation could also be related to environmental situations encountered by an individual in the present or past and could result from the individual's past experiences. Behavioural variation presumably results from how each of these factors influences the benefits and costs of behaviour at a particular time and place. However, a more comprehensive understanding of behavioural variation will emerge only by integrating these different perspectives.

Experiences could influence variables such as size, developmental history and physiological state that are predicted or observed to lead to behavioural differences. Experiences could also influence the individual's perception of its current environmental situation. For example, a fish that recently encountered a predator in a particular location may be less likely to engage in intense aggressive behaviour (Brick 1998, 1999) and spend more time scanning for potential predators than another fish at the same place that has never encountered a predator there.

Early ecological models of behavioural variation assumed that organisms had perfect information about the benefits and costs of behaviour in the situation being investigated (e.g. Charnov 1976). Thus, a forager supposedly knew about size distributions or abundances of prey and the costs of foraging as it selected its diet, but that is unlikely to be the case if those variables change rapidly through time (Dunlap *et al*. 2009). Most organisms undoubtedly do not have perfect information about any situation and some of the variation in behaviour reflects differences in individuals' perceptions of the situation. Experience can reduce future uncertainty by modifying perceptions or expectations of benefits and/or costs in the future (Dall *et al*. 2005). While this variation in uncertainty applies to all types of behaviour, including feeding, antipredator strategies, mating and fighting, we concentrate in this chapter on how experience provides information about benefits and costs of future contests between individuals.

In some contexts involving aggressive behaviour, information might be obtained about potential benefits. For example, how hard a resident male bowl and doily spider fights to maintain access to a female may give a male intruder information about the egg-laying status of the female (Austad 1983). Experience in prior contests presumably may provide information about potential costs of future contests. A prior contest could provide information about an individual's fighting ability and the rate at which it would accumulate costs in a subsequent contest. This reduction in uncertainty of an individual's own fighting ability could then influence how an individual behaves during the subsequent contest. Considerable evidence now indicates that fishes that lose a contest are more likely to lose a subsequent contest (loser effect) and fishes that win are more likely to win a subsequent contest (winner effect) (review in Hsu *et al*. 2006a).

While an individual accumulates information about fighting ability from prior contests, the effect of that information on the outcome of a subsequent contest depends on information accumulated by the other contestant (i.e. its prior experience). The outcome of the later contest depends on information gained by all contestants and how that information influences the ongoing behaviour of each. An important area of current research is how much an individual's behaviour in a contest is influenced by its own information and how much is influenced by the accumulated information of the opponent.

These experience effects on fighting raise numerous questions that are the subject of other current research into the mechanisms and theory of information accumulation. Information that helps an organism predict benefits and costs of a situation should be retained while information that is no longer useful should be jettisoned. But when and for how long is information from a contest useful to the individual? In a highly variable environment, or when fighting ability changes quickly (e.g. high growth rates), information may become outdated very rapidly; in these conditions, we might predict that the effect of experience from a previous contest disappears quite rapidly, especially if maintaining the information has significant costs. The maintenance costs of information could depend on how the information is accumulated. Carriers of short-term information regarding social context, such as hormone titers, may carry significant costs; for instance, persistent elevations in stress hormones (e.g. adrenocorticotropins) or sex hormones (e.g. 11-ketotestosterone) can negatively impact reproduction or immune function, respectively (Kurtz *et al.* 2007; Alsop *et al*. 2009). On the other hand, learning as a long-term mechanism of information accumulation carries costs (Domjan *et al*. 2000) of, for instance, maintaining the new neural

connections, competing uses of those connections and changes in synaptic characteristics (e.g. alterations in receptor expression; Meyer *et al*. 2004). This chapter explores the state of research on cost-related information in animal contests with an emphasis on the role of experience in contest outcomes and points to important areas of future work.

6.2   Information about resource value

Before examining the importance of cost-related information to contest behaviour and outcomes, we first briefly discuss information about resource value. Fishes have been shown to respond to differences in reproduction or survival-related resources and adjust contest decisions accordingly (Arnott & Elwood 2008). Territorial male beaugregory damselfish (*Stegastes leucostictus*), for instance, were more aggressive and delivered more bites to stimulus males when an artificial breeding site was present (Snekser *et al*. 2009). Juvenile convict cichlids (*Archocentrus nigrofasciatus*) adjust their rates of aggression with resource availability, being most aggressive when supplied with intermediate levels of food (Grant *et al.* 2002). Resource expectations can also influence motivation to attack. Dugatkin & Ohlsen (1991) showed that, despite large size asymmetries, smaller pumpkinseed sunfish (*Lepomis gibbosus*) attack first and win more often when trained to expect greater food returns after presentation of a cue. An individual's internal state can also influence its assessment of resource value; the longer the residence of replacement-owner brown trout (*Salmo trutta*), the more intense their contests and the higher the probability of their winning, suggesting that the motivation to defend a territory increases with residence time (Johnsson & Forser 2002). Moreover, the development of reproductive tissue in male cichlid fish, *Tilapia zillii*, better predicted contest outcome than body size (Neat *et al.* 1998a), leading the authors to suggest that differences in gonad development created asymmetries in perceived territory value and caused the males with larger testes to behave more aggressively, persist longer and win more. To strengthen this hypothesis, the authors subsequently showed that winners, losers and controls did not differ in plasma concentrations of testosterone or 11-ketotestosterone, ruling out a difference in androgen levels as the cause (Neat & Mayer 1999). Overall, fishes appear to monitor their environment closely and adjust their contest behaviour readily with changes in the actual or perceived value of the contested resource. Furthermore, their assessment of a resource's value depends not only on its quality or quantity but also on their internal state.

6.3   Information about contest costs

In contests, animals expend energy and time, risk physical injuries and predation and forgo other opportunities (Neat *et al.* 1998b; Brick 1999). An individual's potential contest cost should decrease with its fighting ability and increase with its opponent's, since the more able contestant has the better chance of winning, resolving a contest quickly and avoiding injury (Enquist *et al.* 1990). As expected, contest duration, intensity and outcome vary with competitors' fighting abilities (Enquist *et al.* 1990; Leiser *et al.* 2004; Hsu *et al.* 2008). These studies typically used body or weapon size to index fighting ability because
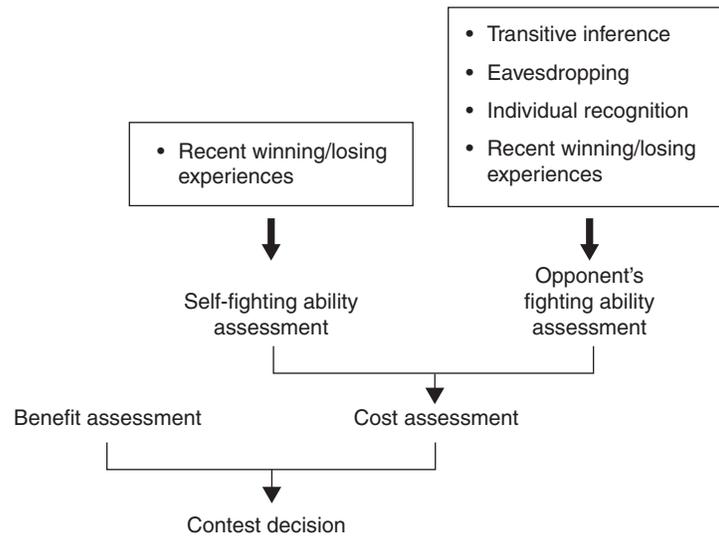
Fig. 6.1 Individuals could use information from various sources to modify their cost assessment for a contest, which subsequently influences their contest decision.

of their correlation with contest success (see Table 2 in Hsu *et al.* 2006a). For instance, in *Kryptolebias marmoratus*, the probability of the larger opponent winning is positively correlated with the difference in the two opponents' sizes while contest duration and intensity are negatively correlated with it (Hsu *et al.* 2008).

Individuals could acquire information about fighting abilities from various sources (Fig. 6.1). An individual could adjust its contest behaviour based on an assessment of its own fighting ability ('self-assessment'; Arnott & Elwood 2009) and/or its opponent's ('mutual assessment'; Arnott & Elwood 2009). Individuals could modify these assessments based on information from previous contests in which they participated or which they witnessed (Hsu *et al.* 2006a).

6.3.1   *Assessing fighting ability*

Differentiating experimentally between whether fishes use self-assessment (where animals make contest decisions based on their own fighting ability alone) or mutual assessment (where they also appraise their opponents' strength) has remained difficult. A significant negative relationship between contest duration/intensity and size disparity was historically regarded as evidence for mutual assessment, on the assumption that the smaller animal retreated more quickly in the face of a much larger opponent (reviewed in Arnott & Elwood 2009; and for fish Enquist *et al.* 1990; Neat *et al.* 1998a). However, this relationship could arise simply because the smaller opponent's size determines contest duration/intensity (the smaller opponent persists or retreats in a contest based on its own energy reserve without assessing the larger opponent's ability) (Taylor & Elwood 2003). To detect mutual assessment, it is necessary, but not sufficient, (see Taylor & Elwood 2003 for discussion of 'cumulative assessment') to show that contest duration/intensity relates positively with the smaller opponent's size and negatively with the larger opponent's size. These conditions,
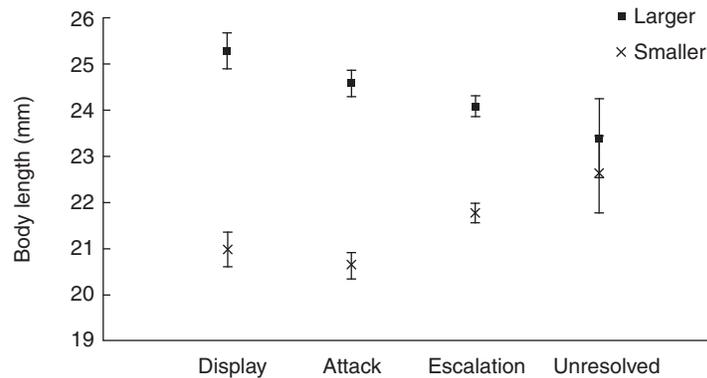
Fig. 6.2 The intensity of contests staged between different-sized individuals of *Kryptolebias marmoratus* depends on the sizes of both opponents; contests between a large larger and a small smaller opponent tend to end after bouts of mutual displays or an attack from the larger opponent while contests between a small larger opponent and a large smaller opponent are likely to progress to escalation (mutual attacks) or remain unresolved after 1 hour. (Data adopted from Hsu *et al*. 2008.)

although they still do not guarantee mutual assessment, provide evidence for the larger opponent influencing the contest.

Following these guidelines, individuals of mangrove killifish (*K. marmoratus*) were found to switch assessment strategy during a contest (Hsu *et al.* 2008). The killifish adopt mutual assessment at earlier stages when deciding whether to escalate a contest from mutual displays to physical interactions (Fig. 6.2); contest intensity is positively related to the smaller opponent's size and negatively to the larger opponent's size. However, the duration of the escalated portion of the contest (involving mutual attacks) is positively related with the loser's size but has no relation with the winner's size. This indicates that the fishes switch to self-assessment once a contest is escalated to physical contact. The killifish has the capability to evaluate an opponent's ability and adjust its contest behaviour accordingly but it does not (or cannot) exercise this ability throughout the entire contest.

However, the assessment strategy of other fish is not as straightforward. In swordtail fish (*Xiphophorus helleri*), although the difference in body size was important for the likelihood of the larger fish winning, the duration of contests between similar-sized swordtails was not associated with the size of the larger or the smaller contestants (Prenter *et al.* 2008). Contest duration correlated negatively with the winner's sword length but had no relationship with the loser's. Therefore, it is not clear whether the fishes assess either their own or their opponents' strength using either body size or sword length. In male convict cichlids (*A. nigrofasciatus*), contests between size-matched opponents showed that large- and small-sized pairs fought for similar durations (Leiser *et al*. 2004) as predicted by the mutual assessment but not the self-assessment hypothesis. However, small pairs adopted different fighting strategies and escalated to biting more quickly than large pairs, showing the importance of opponents' absolute size (not just relative size) to contest strategy; this is not predicted by the mutual assessment hypothesis. Thus, no firm conclusion about the fish's assessment strategy can be drawn from these results.

Based on the few studies summarised above, it appears that different species of fish may adopt different assessment strategies, but the data are not yet sufficient to gain a good sense of the diversity of assessment strategies employed by different fishes, or by the same species in different contexts or during different contest stages. One area suggested by the studies as worthy of further research is whether assessment strategies vary with underlying ecological or evolutionary factors such as social system (e.g. killifish are solitary, swordtails are highly social and cichlids are territorial).

6.3.2   Information from past contests

Contestants may derive information about their fighting ability from contest(s) in the recent past. For instance, outcomes of previous contests could give individuals information about how their fighting ability compares with the overall population (winner and loser effects; Whitehouse 1997). Contestants that have fought before could recognise each other and avoid unnecessary costs by using the outcome of their previous interaction to settle their future conflicts (individual recognition; Tibbetts & Dale 2007). Furthermore, an individual could extract information about the participants' fighting abilities from the interaction in or outcome of contests it has previously witnessed but not taken part in (social eavesdropping; McGregor & Dabelsteen 1996).

6.3.2.1   Winner and loser effects

Many fishes adjust their fighting decisions as a result of the outcomes of their previous contests (Table 1 in Hsu *et al.* 2006a). After a recent win, individuals often become more aggressive (e.g. more likely to initiate contests, retaliate when provoked and persist longer before retreating) and, as a consequence, have a higher probability of winning the next contest. In contrast, after a recent loss, individuals become more passive and likely to retreat sooner when challenged. Winner and loser effects are usually hypothesised to be the result of prior winning and losing experience influencing an individual's assessment of its own fighting ability and its estimated fighting costs in later contests (Whitehouse 1997). Winning experiences appear to raise and losing experiences to lower an individual's perception of its fighting ability. However, not all species display experience effects and not all species whose contest decisions are influenced by past contest experiences display both winner and loser effects. The general trend is that loser effects are detected more frequently, have a stronger impact and last longer than winner effects. In fishes, winner effects have been observed in sticklebacks (*Gasterosteus aculeatus*; Bakker & Sevenster 1983; Bakker *et al.* 1989), mangrove killifish (*K. marmoratus*; Hsu & Wolf 1999; Hsu *et al.* 2009), pumpkinseed sunfish (*L. gibbosus*; Chase *et al.* 1994), Mozambique tilapia (*Oreochromis mossambicus*; Oliveira *et al.* 2009) and blue gourami (*Trichogaster trichopterus*; Frey & Miller 1972). Loser effects, but not winner effects, have also been detected in green sunfish (*Lepomis cyanellus*; McDonald *et al.* 1968), paradise fish (*Macropodus opercularis*; Francis 1983) and African cichlid (*Melanochromis auratus*; Chase *et al.* 2003). Siamese fighting fish (*Betta splendens*; Wallen & Wojciechowski-Metzlar 1985) and steelhead trout (*Salmo gairdneri*; Abbott *et al.* 1985) are reported to exhibit experience effects; however, the experimental procedures used (pitting prior winners against prior losers) did not allow

winner or loser effects to be distinguished. Several studies of green swordtail fish (*X. helleri)* produced mixed conclusions regarding the presence of effects (winner and/or loser effects: Franck & Ribowski 1987; Beaugrand *et al*. 1991, 1996; Beaugrand & Goulet 2000; no experience effects: Earley & Dugatkin 2002).

The magnitude and permanence of winner and loser effects vary considerably among species (Hsu *et al.* 2006a). For instance, the probability of prior winners winning against size-matched, naive opponents ranges from 0.5 (no effect; paradise fish, Francis 1983) to 0.78 (pumpkinseed sunfish, Chase *et al.* 1994) and the effect can decay completely in an hour (pumpkinseed sunfish, Chase *et al.* 1994) or last more than 2 days (mangrove killifish, Hsu & Wolf 1999). The probability of prior losers winning against size-matched naive opponents varies from 0.5 (no effect; green swordtail fish, Earley & Dugatkin 2002) to 0 (sticklebacks, Bakker *et al.* 1989) and the effect can disappear in 24 hours (as suggested by unanalysed preliminary data, Bakker *et al.* 1989) or last more than 3 days (paradise fish, Francis 1983).

Some part of the differences in the magnitude and permanence of experience effects between species and the asymmetrical winner and loser effects within species could result from differences in methodology (see Hsu *et al.* 2006a, 2006b for a more detailed discussion). These differences include the protocol for training animals with winning and losing experiences, the frequency and duration of experience training, the time interval between the completion of experience training and the subsequent contest and whether (and for how long) study animals were isolated before experience training. The procedures used to train animals can be roughly grouped into self- or random-selection. For self-selection, the winner and the loser of a size-matched fight are treated as having a winning and a losing experience, respectively, a procedure which could confound experience effect with intrinsic fighting ability (Chase *et al.* 1994). Bégin *et al.* (1996) concluded that a self-selected winner has a 0.67 probability of having higher intrinsic fighting ability than a size-matched, naive opponent (0.83 if compared with self-selected losers), as opposed to a 0.5 probability as usually assumed and tested. On the other hand, random selection gives predetermined winning or losing experiences to individuals chosen at random by pitting the study animals against smaller, habitual losers or larger, habitual winners, respectively. Studies that employ self-selection procedures and test against a null of 0.5 may, therefore, find statistically significant but bogus winner and loser effects that would not be detected by studies employing random-selection procedures. The difference in the significance of an experience effect detected from these two procedures could be further complicated by the possibility that the 'quality' of an experience depends on the opponent and the interaction with the opponent. A low-quality opponent that is easy to beat may give an individual less information about its fighting ability than a high-quality opponent. Thus, a win/loss against a similar-sized or a much smaller/larger trainer may have different influences on an individual's perceived fighting ability. Because experience training can cause energy depletion, bodily injury and physical exhaustion, prolonged experience training can compromise the physical condition of trained winners and losers and cause winner and loser effects to appear weaker and stronger, respectively, than they really are. Researchers do not usually test for experience effects immediately after completion of the experience training. A long time interval between the completion of experience training and the subsequent contest provides study animals 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. Finally, isolating study animals before experience training could further complicate the interpretation of the observed winner and loser effects. The purpose of this isolation is to allow focal individuals sufficient time for the effects of previous agnostic experience to dissipate. However, one must also consider the varied effects of isolation itself on agonistic behaviour (Gomez-Laplaza & Morgan 2000); depending on species and age, social isolation can lead to increases or decreases in aggressive behaviour.

Asymmetrical winner and loser effects could be adaptive. Engaging in contests but losing may incur more costs (time, energy, injuries) than retreating without confrontation (Neat *et al.* 1998b), which could select individuals that refrain from engaging in contests after a recent loss (i.e. for a stronger loser than winner effect). However, it is also possible that winner effects are simply harder to detect experimentally because of differences in the behaviour of losers and winners when each is faced with a naive opponent (Mesterton-Gibbons 1999). Individuals with prior losing experience often voluntarily retreat from a subsequent contest and lose to their naive opponents (e.g. Bakker & Stevenster 1983). On the other hand, contests between prior winners and naive opponents are more likely to escalate into physical fights, in which prior winners and their size-matched naïve opponents are expected to have an equal chance of winning – if prior contest experience alters only an individual's perceived but not actual fighting ability (Hsu & Wolf 1999). In this case, contest-related behaviours (e.g. escalation rate) that are sensitive to both winning and losing experiences might be more appropriate for measuring experience effects than the probability of winning.

Differences among species in the importance and permanence of experience effects may reflect differences in the usefulness of prior contest information, which should depend on its reliability for use in future contests. Therefore, factors (physiology, ecology, etc.) that influence information reliability may influence the magnitude and permanence of the effect. For example, where size is important to fighting costs, slow-growing species or age groups may retain information from a prior contest longer than those that grow more quickly. For species with indeterminate growth (e.g. fish; Patnaik *et al.* 1994), experience effects may remain transitory for life. The frequency of social encounters might also have an effect (Schuett 1997; Hsu *et al.* 2006a). If outcomes of previous contests offer an individual information about how its fighting ability compares with the overall population (Whitehouse 1997), then individuals in populations with more social encounters will more frequently obtain recent and more reliable information and thus do not need to preserve information from past interactions for as long as individuals in populations with fewer social encounters.

6.3.2.1.1   *Testing the behavioural mechanisms of experience effects*
Winner/loser effects are usually thought to be a consequence of individuals re-estimating their fighting ability after one or more winning/losing experiences and changing fighting behaviour as a result (Whitehouse 1997; Hsu *et al*. 2006a). However, it is possible that prior winners and losers also release status-related cues which opponents can detect and use to adjust their contest strategy. Opponent's use of these status-related cues could enhance the

winner/loser effects (social-cue hypothesis, Rutte *et al.* 2006). Dominant and subordinate individuals of some fishes have been observed to release different chemicals or different quantities of the same chemicals into the water (Oliveira *et al.* 1996; Barata *et al.* 2007). For instance, in the presence of females that are ready to spawn, dominant Mozambique tilapia (*O. mossambicus*) males urinate more frequently and produce more urine than subordinates and their urine has greater olfactory potency (Barata *et al.* 2007, 2008). Furthermore, female tilapia's olfactory system is more sensitive to dominants' urine, which leads the authors to conclude that dominant tilapia males use urine odour to signal dominance to females (Barata *et al.* 2008). Although fishes are clearly capable of detecting and responding to chemical cues released by conspecifics, Hsu *et al.* (2009) did not find evidence to support the social-cue hypothesis; individuals of *K. marmoratus* adjusted their contest strategy based on their own recent contest experiences but not their opponents' experiences. Although not directly tested, the social-cue mechanism probably also does not play an important role in Siamese fighting fish's (*B. splendens*) contest decisions. The fish appears to exhibit experience effects such that individuals with recent winning experiences behave more aggressively and win more contests fighting against individuals with recent losing experiences (Wallen & Wojciechowski-Metzlar 1985). However, bystanders do not respond differently to prior winners and losers that they did not observe fighting (Oliveira *et al.* 1998), suggesting that behavioural cues or other types of cue indicative of status are either unavailable to or unused by bystanders. Thus, the winner/loser effect in Siamese fighting fish appears to operate through individuals changing contest decisions based on their own contest experiences, as in the mangrove killifish. Because this mechanism has not been examined in the other species, it is not clear whether status-related cues contribute to the winner/loser effect in any species. More studies are needed to determine this.

6.3.2.1.2   Integrating information from multiple contest experiences
Only a few studies have examined the effect of multiple contest experiences on future contest behaviour (Hsu & Wolf 1999; Bekoff & Dugatkin 2000; Oyegbile & Marler 2005, 2006). Evidence so far indicates that the effects of different prior contest experiences on behaviour and physiology are cumulative but that they decay with time. In the mangrove killifish, a more recent experience (24 hours earlier) had a stronger impact on contest behaviour than an older one (48 hours earlier) (Hsu & Wolf 1999). However, we know very little about how information from different experiences is combined. For instance, are the effects from different contest experiences additive or multiplicative? If effects are multiplicative, their magnitude is a function of an individual's prior perceived fighting ability and recent contest experiences; if additive, their magnitude is fixed (see Hsu *et al.* 2006a for a discussion).

Another complicating factor is whether the value of an experience is influenced by other experiences (Bouton & Moody 2004; Jonides *et al.* 2008) as well as deteriorating with time (Bakker *et al.* 1989; Chase *et al.* 1994). The memory of an experience may be influenced by older (proactive interference) or newer (retroactive interference) experiences. These are frequently discussed in the learning literature (Bouton & Moody 2004; Jonides *et al.* 2008), but have not been explored in the context of animal contests. If different contest experiences interfere with each other, the combined effect will be different from the sum of the individual effects adjusted for time decay.

6.3.2.2   Individual recognition

The behavioural decisions of shoaling fish and the dynamics of competitive interactions in territorial species are mediated, in part, by the ability of individuals to distinguish among familiar conspecifics (Miklósi *et al.* 1995; Miklósi *et al.* 1997; Griffiths 2003). Individual recognition can reduce fighting costs if the probability of encountering the same individual on a regular basis is high (Pagel & Dawkins 1997; Tibbetts & Dale 2007). In fishes, memory of past opponents is ascertained by comparing the behavioural response of losers when encountering (a) their former dominant and (b) an unfamiliar opponent. Losers generally 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 (Keeley & Grant 1993; Earley *et al.* 2003). It is unclear whether winners fail to escalate because they recognise a former subordinate and/or because the opponent behaves submissively.

Individual recognition and winner/loser effects may contribute to the formation and stability of dominance hierarchies (e.g. Dugatkin 1997; Dugatkin & Earley 2004; Hock & Huber 2009). The importance of recent contest experience on dominance ranks has been demonstrated in green swordtail fish (*X. Helleri*; Dugatkin & Druen 2004). When size-matched males were given winning, losing or no experience and then placed together to form a dominance hierarchy, previous winners were more likely to emerge at the top and prior losers at the bottom. Individual recognition might stabilise dominance hierarchies by reducing aggression among group members (Morris *et al.* 1995; Johnsson 1997; Hojesjo *et al*. 1998). Small hierarchies are generally more linear than large hierarchies (e.g. see Chase 1974), which suggests that where recognition of all group members is possible or where the benefits of recognition strategies exceed the costs (Pagel & Dawkins 1997) distinguishing among individual opponents stabilises the hierarchy.

6.3.2.3   Social eavesdropping

In some fish species, individuals appear to obtain a relatively accurate estimate of possible costs in future contests by social eavesdropping, the act of extracting information from contest interactions between others (Peake & McGregor 2004; Peake 2005; Bonnie & Earley 2007; Valone 2007). This might be particularly advantageous when the costs of physical combat are high (Johnstone 2001). In Siamese fighting fish (*B. splendens*) and green swordtail fish (*X. helleri*), observers appear to update their perception of the watched individuals' fighting abilities 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 (*O. mossambicus*: Oliveira *et al.* 2001) and increases the aggressive behaviour of male *B. splendens* towards unobserved opponents (Clotfelter & Paolino 2003). It is possible that watching fights elicits behavioural

and physiological 'priming' responses (Hollis *et al.* 1995), which cause post-observational changes in agonistic behaviour regardless of the future opponent. However, studies on green swordtail fish indicate that eavesdroppers predictably modify their response towards individuals that they had observed to win or lose, but not towards unobserved animals (Earley & Dugatkin 2002; Earley *et al.* 2005). The response of swordtail bystanders towards winners and losers also indicates that fishes might be capable of rather sophisticated, indirect assessment of fighting ability. Although bystanders avoided confrontation with observed winners, their response towards observed losers depended on how long the loser persisted in the watched contest (bystanders avoid fights with persistent losers; Earley & Dugatkin 2002). This suggests that fish bystanders can cue in on both contests dynamics and outcome and modify their behaviour in future encounters accordingly.

Recent simulation models have addressed whether eavesdropping can combine with winner and loser effects to promote linear dominance hierarchies, and there is some indication that they can (Dugatkin 2001). However, the verdict is uncertain, due in part to unnecessarily strict assumptions including how these experience effects accumulate (e.g. winners can increase perceptions of fighting ability without bound; losers are bound at zero; Earley & Dugatkin 2005).

Transitive inference allows an animal to respond more appropriately to its social environment by combining individual experience with a particular opponent and information obtained through eavesdropping. For instance, if individual A loses to B and then witnesses C defeat B, A may avoid the costs of fighting with C and losing again. Altmann (1981) proposed that non-primate animals were incapable of transitive inference, but pinyon jays (Paz-y-Miño *et al.* 2004), chickens (Hogue *et al.* 1996) and hyenas (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). A fish species (*Astatotilapia burtoni*) has also been demonstrated to be capable of inferring hierarchical relationships from fights that occur around them (Grosenick *et al.* 2007), showing its potential to synthesise social information to guide future contest behaviour.

6.3.3   Integrating different types of cost-related information

As shown above, fishes can adjust fighting strategies based on information that facilitates assessment of their own and their opponents' abilities, previous winning/losing experiences, the identities of the opponents and the opponents' past performances. However, most studies examine the use of only one type of cost-related information. Therefore, it is difficult to find data on whether and how they integrate cost-related information from different sources to arrive at fighting decisions. If prior winning/losing experiences, for instance, provide an individual with information about how its fighting ability compares with the population at large, they would be of limited use to an individual that persists in a contest based solely on its own endurance or energy reserve (self-assessment: energetic war of attrition, Payne & Pagel 1996; war of attrition without assessment, Mesterton-Gibbons *et al.* 1996). Prior contest experiences in this case could still provide the individual useful information such as its energy consumption rate that enables it to decide how long to persist in a contest, although this is not a winner/loser effect. Previous fighting experience might also train individuals to do better in future contests regardless of the outcome of their prior contests

(e.g. Kim & Zuk 2000). Similarly, individual recognition, eavesdropping and transitive inference should be more useful to individuals that adopt the mutual assessment strategy, but have limited value to individuals that adopt the self-assessment strategy.

The magnitude of winner/loser effects on contest decisions is negatively influenced by the discrepancy between the contestants' sizes (Beacham 1988; Beaugrand *et al.* 1991, 1996), indicating that cost-related information from different sources competes to guide contest decisions. It is conceivable that the importance of the information acquired from witnessing contests between other individuals is affected by whether or not the observer has a recent winning or losing experience and by its body/weapon size relative to the previously witnessed opponents. The acquisition and maintenance of the information from different sources may impose different costs on a contestant, and influence which information is used and how long it is retained. For an individual to assess its opponent, for instance, requires it to recognise and respond to characteristics that give a reliable indication of an individual's fighting ability which could divert the individual's attention and compromise its performance in a contest. Eavesdropping and transitive inference require individual recognition, but winner/loser effects do not require such abilities and thus have a lower cognitive requirement, although they do require some physiological mechanisms for the individual to 'remember' the experience (Section 6.4). Activating and maintaining such mechanisms (e.g. elevated testosterone or corticosteroid levels) could involve costs to an individual (e.g. decreased immune system responses; Buchanan 2000; Casto *et al.* 2001). However, they might provide important cost-related information for individuals that do not live in groups and do not encounter the same competitors regularly. As mentioned in Subsection 6.3.2.3, Siamese fighting fish (*B. splendens*) and green swordtail fish (*X. helleri*) appear to update their estimate of the fighting ability of individuals they have observed (Oliveira *et al.* 1998; McGregor *et al.* 2001; Earley & Dugatkin 2002; Brown & Laland 2003). Siamese fighting fish seem to exhibit winner/loser effects (Wallen & Wojciechowski-Metzlar 1985), while evidence for the presence of experience effects in green swordtail fish is equivocal (Earley & Dugatkin 2002). Therefore, it is not obvious whether individuals that are capable of recognising individuals and extracting information from observing contests between others also display winner/loser effects.

Because contestants are likely to obtain and integrate cost-related information from multiple sources, understanding how the information from difference sources interact with each other and are combined to determine contest behaviour should enable us to have a better overview of decision making in animal contests.

6.4   Physiological mechanisms

Decision making during a contest and changes in behaviour that result from information gained in prior wins and losses are modulated through an individual's physiology. During mutual assessment, aspects of an opponent's size, strength and persistence are filtered through the sensory machinery and interpreted through changes in neurochemical processes (e.g. brain serotonergic or dopaminergic activity; Winberg & Lepage 1998). Self-assessment probably entails some way to relay information between gauges of energy reserve (e.g. glycogen stores) or exhaustion (e.g. lactate accumulation) and the neural machinery, which
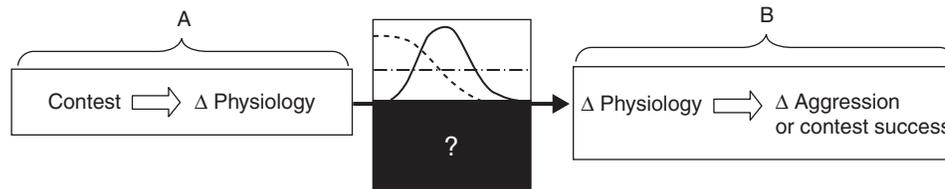
Fig. 6.3 A rich literature has demonstrated that fighting alters an array of physiology parameters (A), and that manipulations of these parameters can cause changes in aggression and/or contest success (B). However, under natural circumstances, animals can engage in multiple interactions over a relatively short time course. The black box with the question mark indicates a void in our understanding of how physiological responses to an initial contest change during an inter-contest interval (three different hypothetical patterns are illustrated), and how the dynamics of this change might impact behaviour and/or success in future contests.

dictates whether an animal persists or gives up in a contest. This basic physiological architecture for decision making in contests could also be modulated in significant ways by changes in endocrine profiles (e.g. androgens, estrogens, glucocorticoids) both during and after a fight. Indeed, post-fight increases in steroid hormones are thought to play an important role in preparing animals to engage in (or avoid) future social interaction (Oliveira 2004). This role for hormones has been supported by an abundance of studies demonstrating that administering hormones prior to a contest predictably modifies behaviour (e.g. androgens elevate aggressive responsiveness: Trainor *et al*. 2004). At this point, we know quite a bit about how the physiology of animals changes after a fight and how altering physiology prior to a fight impacts contest performance. Both during and after fights, an individual's metabolism, endocrine profiles, neurochemistry and neural connectivity/excitability are modified in significant ways. These physiological changes are a source of information about past encounters that animals can use to guide future behavioural decisions. For instance, these changes may facilitate continued exertion/aggression or orchestrate behavioural changes commonly associated with being a winner or loser (e.g. Oliveira 2009). However, we understand very little of how these physiological parameters change temporally between contests (Fig. 6.3; see Summers & Winberg 2006) and how the physiological changes that accompany an initial win or loss influence behaviour and perhaps success (i.e. winner and loser effects) during subsequent contests.

To fully understand this requires time course data for both the winner and loser effects and physiological parameters that could underlie changes in behaviour that are characteristic of these effects. In the vast majority of fish species that have been studied, winner and loser effects disappear quickly (within several days; see Subsection 6.3.2.1). However, few studies have examined winner and loser effects over an extended time course (Hsu *et al*. 2006a) and there is some evidence that prior experiences may have a lasting, background impact on escalation and winning probabilities for up to 1 month (Earley & Hsu 2008). Experience is translated into behavioural change through alterations in physiology and it is likely that a different combination of mechanisms is responsible for short-term (hours to days) versus long-term (weeks to months) changes in aggressive motivation. We forward two very preliminary, non-exclusive hypotheses of how physiological parameters fluctuate between contest experiences, and how these fluctuations might drive the behavioural changes characteristic of winner and loser effects. Each hypothesis maintains that

contests elicit pronounced physiological changes that precipitate modifications to subsequent behaviour. The difference lies in how physiological change translates into behavioural change, and whether learning processes are involved. In the by-product hypothesis, physiological responses during and/or immediately after a contest directly elicit behaviour that increases/decreases the likelihood of winning future contests (non-learning). In the organisational hypothesis, early physiological change(s) may additionally trigger a cascade of events that reorganises neural circuits to maintain behavioural differentiation between winners and losers (learning). It will be important also to integrate these hypotheses with an understanding of the natural history and life history of the organisms being studied; growth rates, type of social system (e.g. shoaling vs. territorial), interaction frequencies in the field and reproductive seasonality could all be superimposed on to these basic models to provide a richer understanding of variation in the existence and permanence of winner–loser effects among species.

Winner and loser effects could arise as a by-product of physiological deviations from baseline in response to fighting experience, and could dissipate rather quickly with subsequent recovery of baseline physiology (by-product hypothesis; Fig. 6.4a). Contestants must mobilise energy stores to maintain high activity levels during a fight, and this often is reflected as depleted glycogen reserves and increased blood glucose levels (e.g. Haller *et al*. 1996; Campbell *et al*. 2005). To fuel metabolic processes and generate energy, fighters also increase rates of oxygen consumption (Ros *et al*. 2006) and, if the contest escalates persistently, they turn to anaerobic metabolism. This switch to anaerobic metabolism results in elevated tissue lactate levels, typically in both contestants (Briffa & Sneddon 2007). Depletion of energy reserves and the accumulation of lactate can constrain the ability of animals to persist in a current contest (Abraham *et al*. 2005) and, depending on recovery times and interaction frequencies, could also limit an animal's ability to engage successfully in future contests. At first glance, changes in metabolic physiology would seem to impact both winners' and losers' future performance negatively, perhaps equally so, and thus fail to explain behavioural differences characteristic of the experience effects. However, if eventual losers accrue metabolic costs at a faster rate than eventual winners (Briffa & Sneddon 2007), and if recovery times are independent of status, then losers might be expected to take longer to restore homeostasis than winners. Thus, we might expect prior losers to refrain from aggressive contests or to give up when challenged over a considerably longer time interval than prior winners, who may fully recover in time for a second interaction shortly after the first. This might explain why, in some species, loser effects exist without a corresponding winner effect, and perhaps why loser effects generally last longer (Hsu *et al*. 2006a).

Another possibility is that eventual winners and losers accrue metabolic costs at the same rate but that some other status-dependent variable intervenes in ways that slow the recovery of losers, thereby leading to pronounced loser effects (and no winner effects). In many fish species, losers exhibit significantly higher plasma concentrations of the stress hormone cortisol than winners (e.g. Øverli *et al*. 1999; Hoglund *et al*. 2000; Sloman *et al*. 2001; but see Earley *et al*. 2006; Earley & Hsu 2008). Following physical exertion (e.g. intense contests), high levels of cortisol can impair lactate recovery and the ability of fish to replenish muscle glycogen stores (Milligan 2003). In this case, the interaction between endocrine parameters and metabolic physiology might constrain the ability of losers to engage in, or win, future contests and thus explain the prevalence of loser effects.
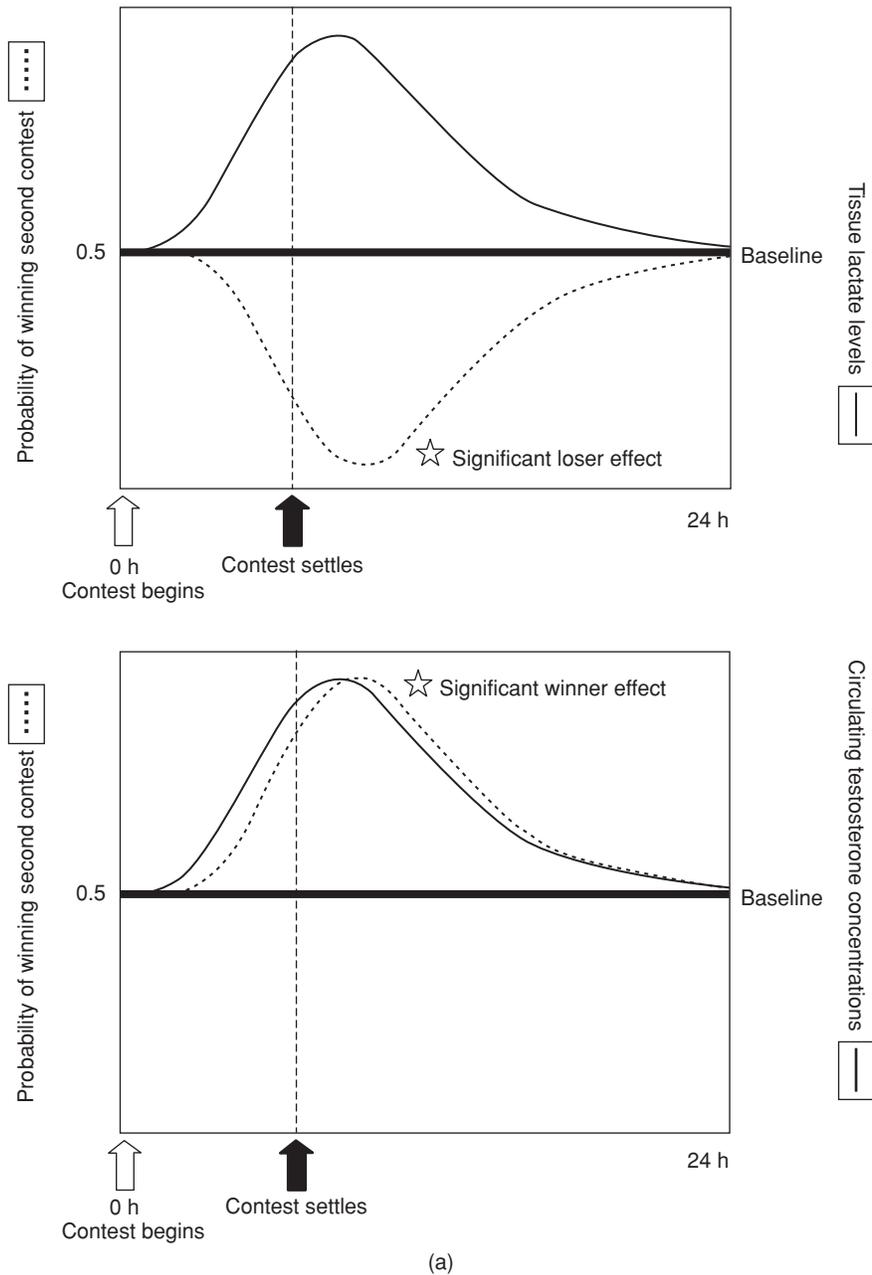
Fig. 6.4 Schematic diagrams representing two basic, non-independent hypotheses for mechanisms driving the winner and loser effects. (a) Two representations of the by-product hypothesis, wherein probabilities of winning a second contest (dotted curve) track changes in physiological parameters that occur as a consequence of winning or losing a first contest (solid curve). These physiological parameters include metabolic constraints on contest performance, such as tissue lactate (top panel), or hormones such as testosterone that activate behavioural responses (e.g. attack initiation) relevant to contest success (bottom panel). Note that in both representations, changes in winning probabilities are short-lived (<24 hours). Winning probabilities refer to the success of an experienced animal (prior win or loss) against a size-matched conspecific opponent encountered at some point following resolution of the initial contest (dotted line). In both panels, the slight lag between hormone/lactate elevations and behavioural change results from the time it takes hormones to bind cytosolic, nuclear, or cell surface receptors and initiate their direct (perhaps non-genomic) actions on behaviour or for lactate to exert its metabolic effects.
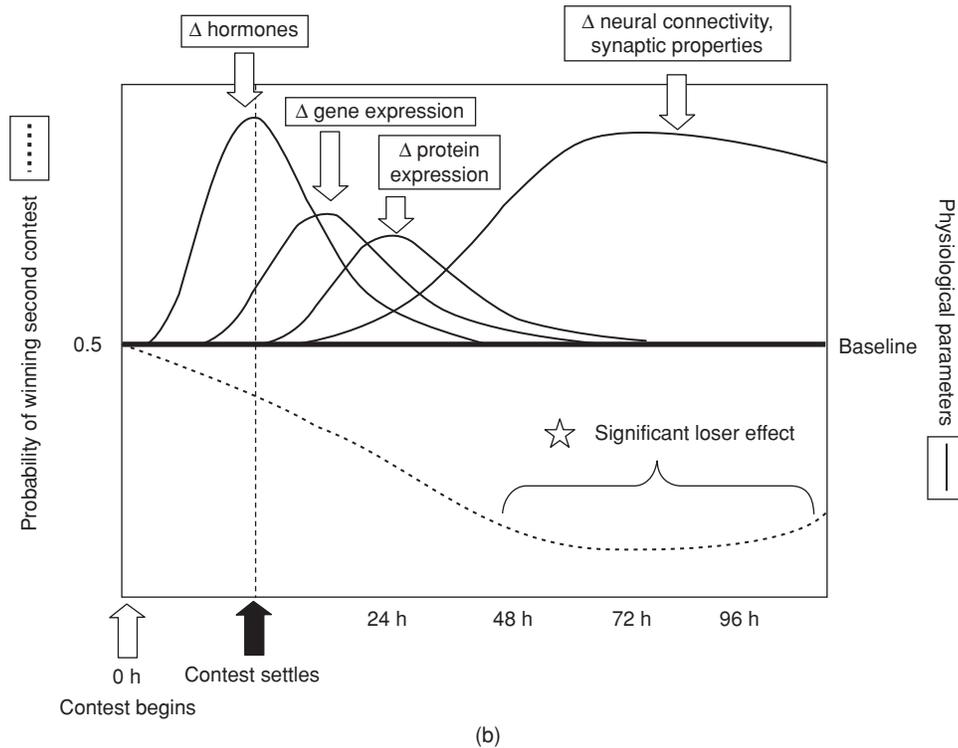
(b)

Fig. 6.4 (*Continued*) (b) A representation of the organisational hypothesis where, for instance, hormone elevations that result from an initial losing experience trigger a cascade of molecular and cellular events that crystallise the effects of experience on future winning probabilities, perhaps for extended periods of time (e.g. >96 hours). The assumption here is that the different physiological parameters (e.g. hormones, gene expression, neural connectivity) are causally and sequentially linked. In this model, the probability of winning may not correlate well with any one parameter (e.g. hormone concentrations, gene expression) because changes in contest behaviour hinge on an integration of various molecular neuroendocrine reorganisations. The temporal trajectories, amplitude of the peaks and order of events shown in these figures (a and b) are not meant to be precise representations of what occurs physiologically; rather, they should be seen as a heuristic for understanding potential relationships between physiology and behaviour.

These ideas on the metabolic correlates of fighting, and their relevance to understanding winner and loser effects, produce at least two important considerations. First, if loser effects are driven largely by changes in metabolic physiology, then we might expect to see variation within species in the magnitude and/or duration of the loser effect. Individuals could retreat immediately or engage in various levels of escalation en route to a loss, and the intensity of the contest will likely impact their physiology in different ways (e.g. individuals who retreat immediately suffer little metabolic cost). Thus, we might expect variation in the magnitude of loser effects to scale in some fashion to the intensity of the initial contest, with losers of metabolically costly contests exhibiting a more pronounced experience effect than losers that incurred little cost. To date, no study has investigated the effects of initial contest dynamics (e.g. whether and for how long the eventual loser was willing to escalate) on the existence or persistence of experience effects. Second, it is often assumed that winner and

loser effects are driven by similar mechanisms acting in opposing fashions. As should be evident from the discussion above, this need not be the case. The accumulation of metabolic costs can explain why prior losers become behaviourally inhibited but cannot explain why prior winners often exhibit aggressive motivation that exceeds that of naive animals.

Winner effects could also arise as a by-product of status-dependent changes in physiology. Fishes in positions of dominance often have higher levels of androgens (e.g. testosterone and 11-ketotestosterone) than subordinates (e.g. Neat *et al*. 1998; Elofsson *et al*. 2000), and aggressive challenges tend to stimulate androgen production (Hirschenhauser *et al*. 2004), although the responses vary among species and contexts. Post-fight elevations in androgen concentrations are thought to prepare individuals to respond more quickly or with greater vigour to future aggressive challenges (Oliveira 2004). This is supported by studies showing that administration of androgens enhances the expression of aggressive behaviour in fishes (Fernald 1976; Trainor *et al*. 2004; Remage-Healey & Bass 2006), and that individuals with higher baseline androgen levels tend to initiate attacks in a contest (Earley & Hsu 2008). Cichlids trained in a classical conditioning paradigm pairing light with territorial intrusion show an anticipatory increase in androgens when presented with light alone, suggesting a critical role for androgens in priming aggression (Antunes & Oliveira 2009). One of the most robust findings related to experience effects is the propensity of prior winners to attack quickly and therefore win subsequent contests. If aggressive motivation is increased only when circulating androgens exceed some threshold, and if the by-product hypothesis holds true, we might expect the winner effect to last only as long as androgen levels remain high. Although significant evidence points to a reciprocal relationship between androgens and contest behaviour (Oliveira 2009), no study has tracked the decay of androgens following an initial contest and mapped this decay onto changing winning probabilities.

An alternative to the by-product hypothesis is that winner and loser effects result from coordinated changes in physiology at multiple organisational levels (e.g. from molecules to cells and tissues) that reorganise neural pathways in the brain in ways that promote adaptive behavioural flexibility in the face of changing social conditions (Fig. 6.4b). These changes constitute potential mechanisms of learning – persistent changes in behaviour that result from past experiences (Shettleworth 1998). Arguably, the most well-documented physiological response to fighting is a change in steroid hormone concentrations (Hsu *et al*. 2006a); levels of stress hormones (e.g. cortisol, corticosterone) and sex hormones (e.g. testosterone, 11-ketotestosterone, estrogens, progesterone) can be altered markedly following a contest, often in a status-dependent manner. These hormones serve purposes other than directly activating behavioural responses (as assumed by the by-product hypothesis) many of which are particularly relevant to winner and loser effects. For instance, elevated stress hormones and aggressive interaction both upregulate NMDA receptor expression in the hippocampus of *Anolis* lizards (Meyer *et al*. 2004); androgens and estrogens can also modulate NMDA receptor activity in the brain (e.g. White *et al*. 1999; Srivastava *et al*. 2008). NMDA receptors bind the neurotransmitter glutamate. The availability of NMDA receptors at a synapse, coupled with the trafficking of AMPA receptors (also glutamate-binding) to the cell surface and the morphology and number of dendritic spines, can mediate synaptic plasticity, learning and memory (Kasai *et al*. 2003). In addition, social interaction and steroid hormones, particularly stress hormones, are known to modulate cell proliferation in the brains of fish, which could also impact learning and memory. For instance, Dunlap *et al*. (2006) paired

brown ghost knife fish (*Apteronotus leptorhynchus*) with a conspecific or treated them with cortisol and compared neurogenesis between these animals and isolates or untreated fishes, respectively. The treated fish showed increased neurogenesis and higher densities of radial glial fibres, along which new cells migrate to their destinations, in behaviourally relevant brain areas (e.g. periventricular zone) compared to the isolates and untreated fish. Sørensen *et al*. (2007) also demonstrated a reduction in cell proliferation in both dominant and subordinate rainbow trout (*Oncorhynchus mykiss*) relative to controls, suggesting that social interaction can affect neurogenesis in diverse ways depending on social circumstance.

Thus, steroid hormones may organise the brain in ways that enhance synaptic strengths or modify cellular constituents in relevant brain areas to modulate learning and memory processes that might be necessary to alter perceived fighting ability following wins and losses. NMDA receptors, AMPA receptors and dendritic spines have been characterised in fishes (e.g. mormyrid and gymnotiform electric fish: O'Brien & Unwin 2006; Harvey-Girard *et al*. 2007; Fortune & Chacron 2009), and there are established techniques for examining neurogenesis. However, the relevance of these factors to complex social behaviour has received little attention in fishes. Examining steroid- or status-dependent changes in the expression and/or activity of glutamate receptors, the morphology and turnover of dendritic spines or adult neurogenesis, and the time course of these changes following experience, could be a lucrative area for future study to determine mechanisms underlying winner and loser effects. Goodson (2005) proposed a cross-taxonomic vision of a 'social behaviour network' that includes interconnected brain regions such as the preoptic area, medial amygdala and lateral septum (fish's ventral telencephalic nuclei) and periaqueductal gray, all of which are responsive to steroids and are implicated in the control of many forms of social behaviour. This social behaviour network could serve as an excellent starting point for isolating region-specific, experience-induced changes in brain neurochemistry or morphology that might impact future contest decisions.

Lastly, engaging in aggressive interactions could change gene expression patterns, alter the secretion of neuromodulators, or modify steroid receptor densities to make animals more or less sensitive to their endocrine milieu or prone to respond to social stimuli in an excitatory manner. In the African cichlid, *A. burtoni*, dominant males showed elevated androgen receptor mRNA expression in the anterior portion of the brain (which contains several regions associated with the social behaviour network) relative to subordinates (Burmeister *et al*. 2007). Given that steroid receptors are necessary for hormones to exert their actions on behaviour, it is possible that changes in receptor expression could result in prior winners being more sensitive to androgens than prior losers. Thus, even in the absence of marked changes in hormone production between winners and losers following a contest (e.g. Earley & Hsu 2008), differences in receptor availability could contribute to the 'winner phenotype' (e.g. increased attack motivation). Indeed, prior winners whose androgen receptors were blocked failed to initiate and win future contests although untreated winners still did (Oliveira *et al*. 2009). Fighting experience may also induce changes in the secretion of peptide neuromodulators such as corticotropin-releasing factor (CRF) and arginine vasotocin (AVT) and monoamines such as serotonin (e.g. Winberg & Lepage 1998), which can alter neuronal sensitivity, neurotransmission and future behaviour. For instance, rainbow trout administered CRF shows higher aggressive motivation during contests (e.g. reduced attack latency; Carpenter *et al*. 2009) and damselfish (*S. leucostictus*) treated with intermediate

doses of AVT showed significant elevations in aggressive behaviour (Santangelo & Bass 2006).

The precise mechanisms driving changes in behaviour and contest outcome that characterise winner and loser effects probably represent some combination of the factors described above. Although complex interactions may occur among steroids, neuromodulators, neurotransmitters, receptors and metabolism, this should not dissuade us from investigating the mechanistic bases of winner and loser effects. These effects may arise as a by-product of physiological processes, as an adaptive response coordinated by a multitude of temporally associated endocrine and neural processes or perhaps both, depending on the species, stage of development and social and/or environmental context. Based on the current evidence, it is quite possible that early post-contest changes in physiology (e.g. hormone titres) trigger both immediate behavioural change and organisational processes that crystallise experience leading to long-term alterations in contest behaviour. It is also conceivable that long-term shifts in contest behaviour occur only after an animal has integrated many consistent experiences (e.g. several losses in a row). One could expand upon Fig. 6.4b to incorporate how individual physiology and behaviour are modulated by successive experiences, perhaps at different intervals. Exploring these possibilities will probably yield fascinating insights into the neurobiology of learning and aggression and the interconnectedness of physiological systems that drive behaviour. Comparative approaches might also provide clues into the diverse ways that selection shapes individual responses to fighting experience.

6.5   Conclusions and future directions

More information is accumulating about how experience effects influence subsequent contests. Most studies confirm that prior contest experiences, whether as a participant or an observer, have some degree of influence on the course of future contests, but also show that these effects vary in magnitude and persistence. The obvious conclusion from the accumulating data is that the relationship between experience and contest behaviour is complex and appears to vary at all levels, not only among species but also within individuals over time. The recognition of complexity in experience effects is hardly surprising, but it does focus attention on the need for more diverse studies that will permit attempts to test possible generalisations.

Hypothesised generalisations are most likely to derive from carefully chosen experiments using a variety of fish species reflecting differences in such characteristics as population sizes, group sizes, growth rates and the types of resources for which individuals are competing. Comparison among these studies also will be facilitated by standardisation of methods. Currently, variation in such things as how experiences are given, when subsequent contests are staged and what variables are measured makes it difficult to compare results.

Variables used to measure experimental outcomes should be carefully chosen for their value in discriminating between hypotheses. This means that it is important to define or understand what each variable measures. Items such as contest outcome and the duration of a total contest or of specific stages such as escalation are often analysed. Contest duration is controlled by the loser, so what does it tell us about the winner? And what determines when the loser will retreat? Some models assume that duration reflects depletion of the loser's

fighting resources while others assume that the loser assesses its probability of winning before deciding to quit. The physical interaction in an escalated contest presumably gives the contestants accurate and up-to-date information about their opponents' real fighting ability. Does this mean that their prior experience will have less influence on the outcome of escalated contests?

Prior experience is only one of many possible factors influencing contest outcome. So far most investigations of experience effects have matched opponents for size, although size differences are a very significant predictor of contest outcomes. A few recent studies have also begun to examine the important question of whether fishes follow self- and/or mutual assessment in determining contest strategies. However, very little research has been carried out on how these multiple influences combine to understand how much and when each factor impacts the outcome. Presumably individuals' ability to integrate information from multiple sources varies with the marginal value and reliability of the additional information and the cost of obtaining and storing it. Following on the work of Beaugrand *et al.* (1991, 1996), who integrated size difference and prior experience, we need more experiments that manipulate more than one possible source of information.

This chapter has not mentioned sex or age differences as variables associated with experience effects, primarily because they have not been examined. Differences in benefits of fighting, possible hormonal correlates and even fitness costs of fighting suggest more attention should be directed to female fish. The fact that some fishes are hermaphrodite or change sex might facilitate experiments that provide significant insights into various physiological ways in which sex influences contest behaviour. Fishes of different ages may also respond differently to experience, perhaps due to variations in benefits and costs of fighting or to physiological differences.

Understanding how information is integrated from various sources will depend in part on shedding light on the underlying physiological mechanisms. So too will our understanding of the persistence of experience effects and their relative importance in determining the outcome of later contests. To date, the preponderance of research on physiological mechanisms has focused on steroid hormones. As the research moves forward, it is essential that we study a greater variety of potential mechanisms, including metabolic parameters, neuromodulators, neurogenesis and patterns of gene and protein expression specific to particular brain regions. These mechanisms should ideally be examined not just individually, but in combination with each other and to see how they vary with other components of the phenotype such as morphology. Furthermore, since most such mechanisms affect a wide variety of behaviours, variations in contest behaviour among species, or among individuals in different circumstances, may have evolved because either different responses confer advantages on animals with, for example, different social systems, or because the same mechanisms are affected by selection acting on other traits, either constraining or relaxing constraints on responses to aggression (Ketterson *et al*. 2009). Therefore, future studies that address contests from an integrative perspective will help to shed light on individual- and species-level variations in contest behaviour.

Fishes generally are considered to be good subjects for contest research because they regularly fight, have been shown to respond to complex information from many different sources and are easy to work with experimentally. We still know relatively little about how information from multiple sources is assimilated, how contest behaviour varies with species'

ecology, about the physiological mechanisms underlying experience effects or about the relationship between these questions. Nevertheless, fishes are excellent organisms for these investigations and the field seems poised to make important advances in the next few years. Carefully focused studies should lead to a much better understanding of fighting behaviour, physiological mechanisms and contest outcomes.

Acknowledgements

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