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Learning your own strength: winner and loser effects should change with age and experience

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Winner and loser effects, in which the outcome of an aggressive encounter influences the tendency to escalate future conflicts, have been documented in many taxa, but we have limited understanding of why they have evolved. One possibility is that individuals use previous victories and defeats to assess their fighting ability relative to others. We explored this idea by modelling a population of strong and weak individuals that do not know their own strength, but keep track of how many fights they have won. Under these conditions, adaptive behaviour generates clear winner and loser effects: individuals who win fights should escalate subsequent conflicts, whereas those who lose should retreat from aggressive opponents. But these effects depend strongly on age and experience. Young, naive individuals should show highly aggressive behaviour and pronounced loser effects. For these inexperienced individuals, fighting is especially profitable because it yields valuable information about their strength. Aggression should then decline as an individual ages and gains experience, with those who lose fights becoming more submissive. Older individuals, who have a better idea of their own strength, should be more strongly influenced by victories than losses. In conclusion, we predict that both aggressiveness and the relative magnitude of winner and loser effects should change with age, owing to changes in how individuals perceive their own strength.

Keywords: winner effect; loser effect; state-dependent aggression; dynamic model; Hawk–Dove game

1. INTRODUCTION

Animals compete aggressively over a variety of resources, including food, mates and territories. The study of such conflicts is a key area of research in behavioural ecology, with a rich history of exchange between theory and empirical work (Riechert 1998). Much of this literature is based on predictions of the simple Hawk–Dove game (Maynard Smith & Price 1973), in which it is typically assumed either that competing individuals have equal strength, or that they have perfect knowledge of any asymmetry between them (e.g. a difference in size; Parker 1974; Maynard Smith & Parker 1976; Hammerstein 1981). Here, we explore how animals should deal with conflicts when they are uncertain of their own fighting ability. Our focus is on aggressive behaviour over a series of contests with different opponents, rather than during the course of a contest with a single opponent (reviewed in Arnott & Elwood 2009).

An enduring puzzle in the study of conflict is the widespread existence of winner and loser effects (reviewed in Hsu *et al.* 2006; Rutte *et al.* 2006), in which the experience of winning a conflict makes an individual more likely to win a subsequent conflict, whereas the experience of losing makes it more likely to lose (Chase *et al.* 1994).

Physiological studies in a range of taxa suggest that hormonal (e.g. androgen) or neuromodulator (e.g. serotonin) changes might mediate these effects (Wingfield 1994; Huber & Delago 1998; Oyegbile & Marler 2005; Oliveira *et al.* 2009), but their adaptive basis remains unclear (Hsu *et al.* 2006; Rutte *et al.* 2006). In the absence of any changes in actual fighting ability, why should the outcome of one contest influence the outcome of another?

The key to understanding this problem may be that in real conflicts, the contestants are unlikely to have perfect knowledge of their relative fighting ability. Given this uncertainty, each individual might use the outcomes of previous contests as a source of information, such that experiences of winning and losing alter how it perceives its own fighting ability relative to others in the population (Whitehouse 1997; Mesterton-Gibbons 1999) and, therefore, the expected cost of engaging in an additional fight (Hsu *et al.* 2006). According to this hypothesis, the contestants should modify their aggressive tendencies accordingly. This idea fits with detailed analysis of contests in the killifish *Kryptolebias* (formerly *Rivulus*) *marmoratus* (Hsu & Wolf 2001; Hsu *et al.* 2009), in which previous winning and losing experiences affect the tendency to escalate a confrontation into a physical fight, but have no influence on the outcome of the fight once escalation has occurred.

While many theoreticians have investigated the consequences of winner and loser effects for the formation of dominance hierarchies (e.g. Dugatkin 1997; Bonabeau

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et al. 1999; Hemelrijk 2000; reviewed in Lindquist & Chase 2009), only two previous models (Mesterton-Gibbons 1999; Van Doorn *et al.* 2003*a*,*b*) have looked into how such effects might evolve in the first place (though see Johnstone 2001 for a model in which winners are more likely to win again because of information transmitted to future opponents through eavesdropping). Mesterton-Gibbons (1999) considered a round-robin competition among triads of animals with randomly determined fighting abilities. The individuals in the triad were unaware of their true fighting ability, but had a subjective perception of this which determined the outcome of fights: the chance of winning increased with the extent to which an individual's self-perceived fighting ability exceeded that of its opponent. Regardless of the outcome of a fight, each combatant incurred a cost proportional to the amount by which it overestimated its own fighting ability. Under these assumptions, Mesterton-Gibbons showed that selection could favour winner and loser effects, with individuals raising their self-perceived fighting ability after winning a fight and lowering it after losing.

A more recent treatment by Van Doorn *et al.* (2003*a*,*b*) showed that winner and loser effects could evolve even without differences in fighting ability, as a convention for settling disputes. They considered repeated Hawk–Dove games between a pair of contestants, in which the memory of past victories and losses was limited to the last interaction with that opponent. Multiple evolutionary equilibria were found, including a 'dominance' equilibrium with winner and loser effects, but also a paradoxical 'alternating' equilibrium in which losers tended to attack in the next encounter whereas winners withdrew (Van Doorn *et al.* 2003*a*). Van Doorn *et al.* (2003*b*) then extended this approach to consider interactions among larger groups of individuals, but again involving recall of specific opponents. As before, several types of conventions were found to be evolutionarily stable, including one based on winner and loser effects. In both versions of their model, evolution was more likely to lead to the equilibrium with winner and loser effects when asymmetries in fighting ability were included (Van Doorn *et al.* 2003*a*,*b*).

Here, we take a different approach by modelling a population in which individuals can interact with many different opponents. The individuals in this population vary in strength, but do not know this directly. We investigate the evolution of aggressive behaviour when individuals can remember the outcome of previous fights, but do not recall specific opponents. Our model shows that selection favours 'generalized' winner and loser effects, in which previous fight outcomes influence the tendency to escalate conflicts with opponents who are unfamiliar (even if they have been encountered previously). In addition, we find that the magnitude of these effects changes with age and experience, as does the overall level of aggression.

2. THE MODEL

(a) *Set-up of the model*
We consider an infinite population in which some individuals (proportion p_1) are strong while others (proportion $p_0 = 1 - p_1$) are weak. For the sake of simplicity, we assume that an individual's strength is fixed throughout its lifetime. Events occur in discrete steps of time ('rounds'). Each round, individuals are paired at random to compete over resources of fixed value v. Contests are modelled according to the classic simultaneous Hawk–Dove game (Maynard Smith & Price 1973), in which each individual can choose either to escalate the contest (i.e. play Hawk) or withdraw from any escalation (i.e. play Dove). When the two contestants both play Dove, they share the resource, with each getting a pay-off $v/2$. When one plays Hawk while the other plays Dove, the former gets the resource (pay-off v), while the latter gets nothing (pay-off 0). When both play Hawk, the contest escalates into a physical fight, in which the winner gets the resource (pay-off v), while the loser incurs a fixed injury cost c. The outcome of a fight is influenced by the relative strengths of the two opponents (Parker 1974; Maynard Smith & Parker 1976): strong individuals defeat weak individuals with probability $1 - \gamma$ ($0 \leq \gamma \leq 0.5$), while two opponents of the same strength have an equal chance (0.5) of winning. At the end of each round, a randomly selected proportion d of individuals dies (or drops out of the pool of competitors) and is replaced by naive individuals with no prior experience of fighting.

A central assumption of our model is that individuals lack direct knowledge of their own strength and that of their opponents. However, they retain two pieces of information about the outcome of their previous contests: f, the number of contests that escalated into a physical fight; and n, the number of those fights that they won ($0 \leq n \leq f$). They remember nothing about non-escalated contests. We assume that memory is limited; individuals remember the outcome of the first F fights and then remember nothing more, so $0 \leq f \leq F$. Our results are, however, largely unaffected by this constraint since we set F sufficiently high that an individual is almost certain to die or drop out of the pool of competitors before the limit is reached.

We focus on the probability that an individual plays Hawk given that it won n of its previous f fights, which we write as $P_H(f, n)$. A strategy specifies an array of these probabilities covering all possible situations in which an individual can find itself, i.e. all possible combinations of f and n (where $0 \leq f \leq F$ and $0 \leq n \leq f$). Our aim is to find an evolutionarily stable strategy (ESS; Maynard Smith 1982) for aggression—a strategy that, when adopted by all members of the population, cannot be bettered by any rare, mutant strategy (and is therefore the best response to itself). Given an ESS, we can then measure winner effects as the change in P_H after winning a fight, i.e. $P_H(f + 1, n + 1) - P_H(f, n)$, and loser effects as the change in P_H after losing a fight, i.e. $P_H(f + 1, n) > - P_H \leq ft(f, n)$.

(b) *Finding the ESS*
The success of any given strategy depends critically on the strategies of the opponents encountered. Ultimately, we seek an ESS that is optimal for an individual, given that it is adopted by other members of the population, i.e. a strategy that is a 'best response' to itself. To derive such an ESS, we need to be able to determine the best response to any given population-wide strategy. Consider, then, a

population in which the chance that a randomly encountered weak opponent plays Hawk is h_0 ($0 \leq h_0 \leq 1$) and the chance that a randomly encountered strong opponent plays Hawk is h_1 ($0 \leq h_1 \leq 1$). These values result from the particular strategy $P_H(f, n)$ that the population follows, and reflect the fact that weak and strong opponents may show different aggressive tendencies purely because of their past experiences, even though they are following the same strategy and (like the focal individual) do not know their own strength directly. In appendix A in the electronic supplementary material, we show how, for any given pair of probabilities h_0 and h_1, we can calculate the chance that an individual with n victories in f previous fights will defeat a randomly encountered opponent who plays Hawk. This can then be used to derive the best-response strategy, as explained below.

Starting from a population with arbitrarily chosen values for h_0 and h_1 (resulting from some particular population-wide strategy that we need not specify), we converged on the ESS using an iterated, damped best-response procedure (see Houston & McNamara 1999), incorporating errors in decision-making (McNamara *et al*. 1997). This involved three basic steps: (i) given h_0 and h_1, we derived the error-prone best-response strategy for a single mutant individual in the population; (ii) we then calculated the best-response values of h_0 and h_1, called h_{0b} and h_{1b}, to which this mutant strategy would give rise if it were adopted by the whole population; and (iii) we updated h_0 and h_1 to make them more similar to the best-response values (specifically, we used new values $h_0' = (1 - \lambda)h_0 + \lambda h_{0b}$ and $h_1' = (1 - \lambda)h_1 + \lambda h_{1b}$, with the value of λ set at the start of the procedure). These steps were repeated until a stable solution was reached. At this point, the strategy represents an individual's error-prone best response to the values of h_0 and h_1 that result when others in the population adopt the same strategy, and it is therefore an ESS. We outline the procedure in more detail in appendix A in the electronic supplementary material.

3. RESULTS

We used a value of $\lambda = 0.1$, which allowed smooth convergence to the ESS. In all cases, a unique stable state was found, regardless of the starting values of h_0 and h_1. For the results shown below the default parameter values were $v = 1$, $c = 1$, $\gamma = 0.1$, $p_0 = p_1 = 0.5$, $d = 0.1$ and $F = 30$, but the qualitative patterns we describe are robust to changes in these values. Importantly, the boundary effects resulting from a fixed memory size are negligible (e.g. the ESS for $F = 50$ is almost identical to that for $F = 30$, with the individual probabilities differing by 0.0004 ± 0.0002 (mean $\pm$ s.e.)).

(a) *Winning and losing experiences modulate aggression*

Figure 1*a* depicts the ESS for individuals that have won n out of f previous fights. As expected, the behaviour they adopt depends on their previous experiences: individuals that have won more fights tend to be more aggressive than those that have won fewer fights. There is a clear separation between these two levels of aggression, as shown by the division of the strategy space in figure 1*a* into

two distinct regions. Excluding the states immediately above and below the dividing line, individuals either nearly always play Hawk ($P_H \geq 0.999$ for the parameter values shown) or nearly always play Dove ($P_H < 0.001$). Early experiences are critical; naive individuals are highly aggressive ($P_H(0, 0) > 0.999$) and remain so if they lose their first fight ($P_H(1, 0) = 0.999$), but if they lose their first two fights they become submissive ($P_H(2, 0) = 0.299$) and if they lose a third they refuse to escalate future conflicts at all ($P_H(3, 0) < 0.001$, compared with $P_H(3, 1) > 0.999$, $P_H(3, 2) > 0.999$ and $P_H(3, 3) > 0.999$ if they win any of their first three fights). Increasing the value of the resource (higher v) or reducing the mortality risk (lower d) makes individuals willing to sustain more defeats before becoming submissive (see appendix B in the electronic supplementary material), but we still see a sudden switch to non-aggressive behaviour beyond a certain point. For instance, when $v = 2.2$, individuals continue to be aggressive until their seventh successive defeat, whereupon they adopt more Dove-like behaviour (appendix B in the electronic supplementary material).

Such flexible adjustment of aggression is favoured because the outcomes of fights provide individuals with information about their own fighting ability, which determines the benefits of escalating future fights. Figure 1*b,c* shows the distribution of weak and strong individuals, respectively, across the state space (all combinations of f and n) in the equilibrium population. Statistically, individuals that lose a given fight are more likely to be weak (or, equivalently, less likely to be strong) than if they had won that fight. Excluding the newly recruited fraction d of replacement individuals, the average strong individual has had 6.50 escalated fights and won 4.16 of those, compared with 3.53 fights and 0.85 wins for the average weak individual. For weak individuals (figure 1*b*), the most common experience (22% of individuals) is to lose their first three fights ($f = 3$, $n = 0$); they then get 'stuck' in this state, since they stop playing Hawk and thereby avoid further opportunities to test their strength in additional fights. A smaller fraction (12%) win one or more of their first three fights (often by defeating a weak opponent) and then continue to learn by playing Hawk, but as soon as they enter the non-aggressive part of strategy space (light-coloured region in figure 1*a*), they get 'stuck' by switching to Dove and will learn nothing more (except through occasional errors). Strong individuals (figure 1*c*), in contrast, are much more spread out over state space because they tend to win fights and therefore persist in playing Hawk, which means they continue to gather information on their own fighting ability in escalated contests. Just as for weak individuals, however, as soon as they lose enough fights to push them into the non-aggressive part of strategy space, they get 'stuck' and learn nothing more.

Behaviour under the ESS shows substantial winner and loser effects. For an individual selected at random (with respect to its state f, n), its probability of playing Hawk increases by 0.271 after winning an escalated fight and decreases by 0.102 after losing (averages across all combinations of f and n, weighted by frequency). This change in behaviour affects the individual's chances of procuring the next resource item it contests: a win raises the probability of getting the
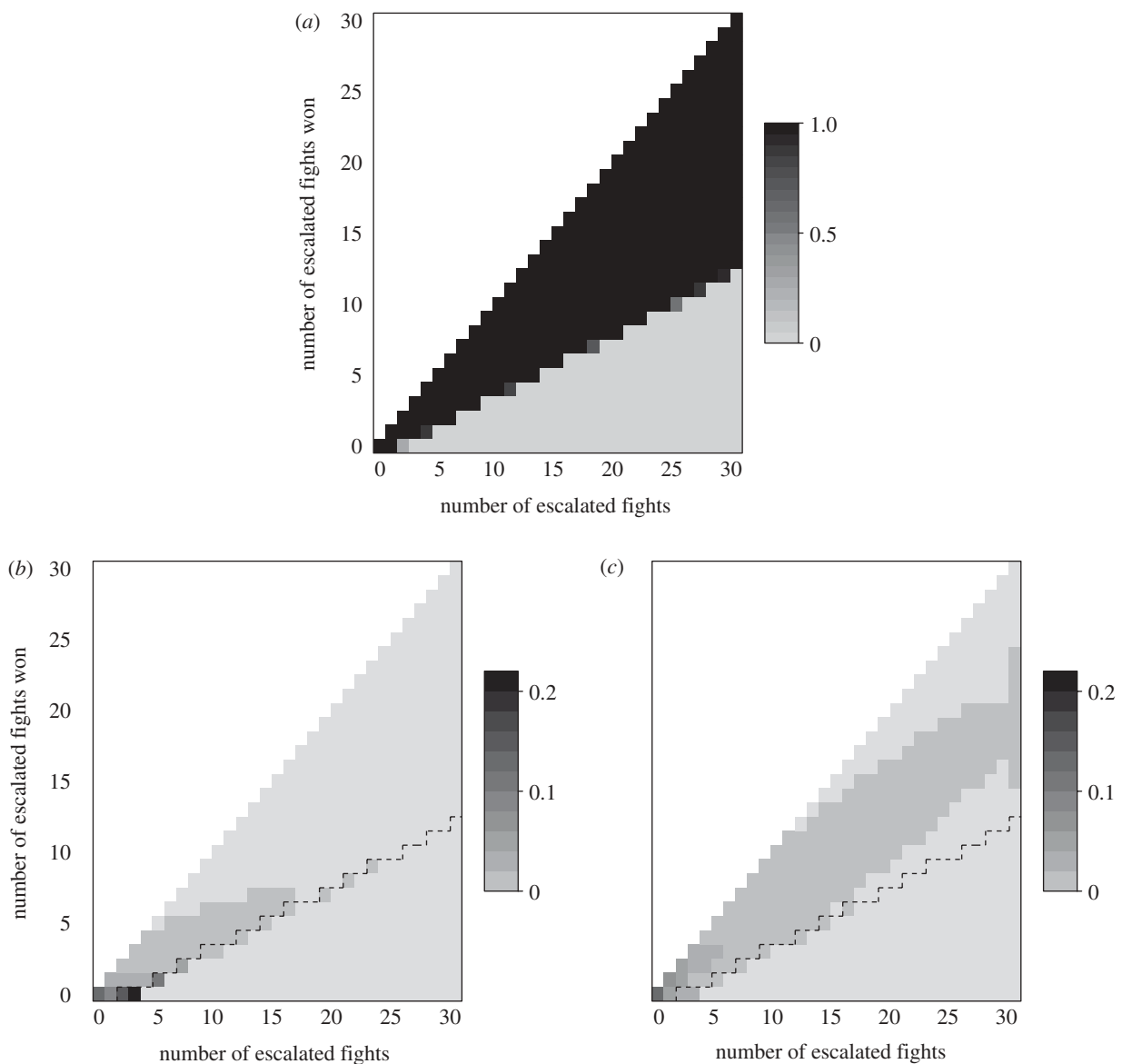
Figure 1. (*a*) The ESS for experience-dependent aggression, showing the probability of playing Hawk for individuals that have previously won n out of f escalated fights. Darker colours indicate higher probabilities. (*b*) The equilibrium distribution of weak individuals across this strategy space, shown as the proportion of those individuals in each state (i.e. each combination of f and n). Darker colours indicate higher proportions. The dotted line marks the switchpoint between aggressive ($P_H \geq 0.5$, above the line) and non-aggressive ($P_H < 0.5$, below the line) behaviour as identified from panel (*a*). (*c*) The equilibrium distribution of strong individuals. Parameter values are given in the main text.

next item by 0.137 on average, whereas a loss reduces it by 0.061. The relative impact of wins and losses changes with different parameter values, the former predominating when v is low and the latter when v is high, but the presence of both effects is a consistent feature of our model. Thus, as emphasized by Hsu *et al*. (2006), winner and loser effects can emerge purely because previous victories and defeats alter individuals' perceptions of their own fighting ability, without any change in actual fighting ability (which was fixed in our model).

Changing the values of the parameters v, d, γ and p_1 changes the position of the dividing line between aggressive and non-aggressive behaviour in the ESS, but the qualitative patterns described above stay the same (see appendix B in the electronic supplementary material). When the resource contested is of greater value (higher v), individuals will sustain a higher proportion of lost

fights (lower n, for a given number of fights f) before they switch to playing Dove. The same is true for lower per-round mortality rates (lower d), bigger fighting advantages to strong individuals (lower γ) and populations in which strong individuals are more common (higher p_1).

(b) *Fighting has information value*
In providing a means by which individuals can assess their own strength, fighting might be beneficial in terms of information, aside from any potential gains in terms of resources. We quantified this information value by calculating, for each state (f, n), the average change in expected future fitness after engaging in one more fight (see appendix C in the electronic supplementary material for details of the calculation). The resulting values are plotted in figure 2. Individuals that have won many fights or lost
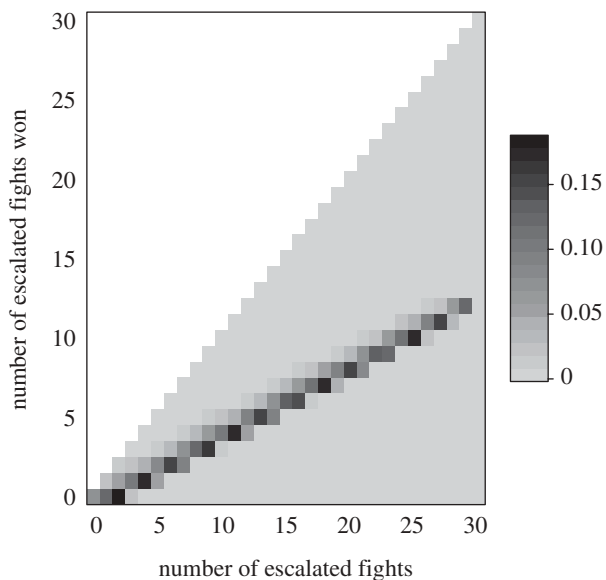
Figure 2. The information value of fighting for individuals in different states, calculated as the average change in their expected future fitness from engaging in one more fight. Darker colours indicate greater fitness gains. Parameter values are given in the main text.
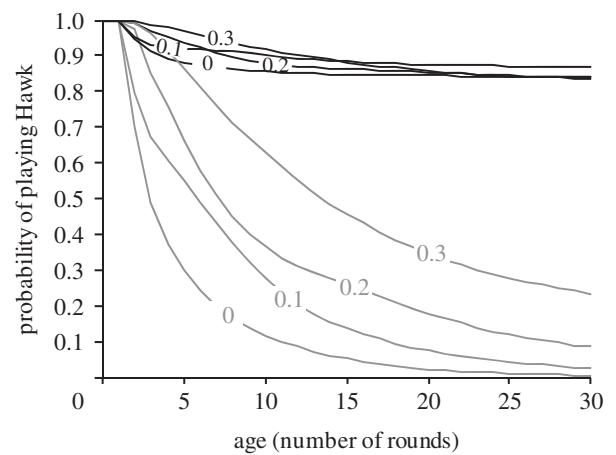

Figure 3. Age-dependent levels of aggression, shown as the average probability of playing Hawk for strong (black) and weak (grey) individuals that have experienced a given number of rounds. The numbers on the lines indicate the chance (γ) that a weaker individual defeats a stronger individual in a fight. Other parameter values are given in the main text.

many fights can be fairly certain of their fighting ability and therefore have little to learn, but for intermediate levels of success, the acquisition of information during a fight can raise future fitness expectations. Specifically, individuals in states along the dividing line between aggressive and non-aggressive behaviour, whose mixed success in previous fights leaves them uncertain about their own fighting ability, enhance their future fitness by fighting again. This is also the case for naive individuals ($f = 0$, $n = 0$), who lack any information on their fighting ability and therefore benefit by being aggressive, separately from any resources they stand to gain.

(c) Aggression should change with age and experience

The newly recruited individuals (fraction d) start out with a high level of aggression, but how does this change as they age and gain experience? We investigated this by tracking a cohort of these individuals over time, calculating their changing distribution across state space and determining their resulting behaviour. Time in our model is divided into discrete rounds, which allows us to express the age of an individual as the number of rounds since it first entered the interacting population. (Note that while every round involves a new encounter, this only provides information if it develops into a physical fight; thus age is not equivalent to fighting experience.) As shown in figure 3, aggression is at its highest at the point of recruitment, when the individuals are naive with respect to their own fighting ability and information is particularly valuable. It remains high for the first two rounds but then declines over their lifetime as they gain information, with those losing fights switching to non-aggressive (Dove) behaviour in which they retreat from aggressive opponents before escalation occurs. Thus, according to our model, aggression is highest on average in young individuals because they are uncertain of their own fighting ability. The subsequent drop in aggression

is steepest for weak individuals, since these tend to lose more fights, but both types of individuals become less aggressive with age. The weak and strong trajectories diverge most at low values of γ, which ensure that strong individuals seldom lose to weak individuals, and therefore that the outcomes of fights are particularly informative (figure 3).

In fact, the levels of aggression shown by young individuals are so high that they have little capacity to increase further. Consequently, loser effects (calculated as the drop in P_H after losing a fight) are more powerful for these individuals than winner effects (the rise in P_H after winning a fight). As individuals age, however, this situation reverses (figure 4); for older individuals, victories have a bigger impact than losses. This makes sense if we consider the distribution of individuals across the state space (figure 1b,c). Several rounds after first entering the population, the majority of individuals are likely to find themselves in one of two general situations. Some individuals, most of them weak, lost their first few fights and consequently switched to non-aggressive behaviour (low P_H), leaving them 'stuck' just below the dividing line with more aggressive behaviour (high P_H). If these individuals do happen to get into another fight, losing again will have little impact because they will remain non-aggressive, whereas a win will push them over into the highly aggressive part of strategy space (dark region, figure 1a). The other main group of individuals, most of them strong, won their early fights and continued to be aggressive, allowing them to obtain further information and become more certain of their own fighting ability. These individuals now find themselves spread out over the highly aggressive part of strategy space, and apart from those just above the dividing line with non-aggressive behaviour, an additional win or loss will make little difference to their behaviour. In short, individuals that remain aggressive gather enough information to be fairly certain of their own fighting ability, whereas those losing early fights are less well informed and are therefore strongly affected by an unexpected victory.
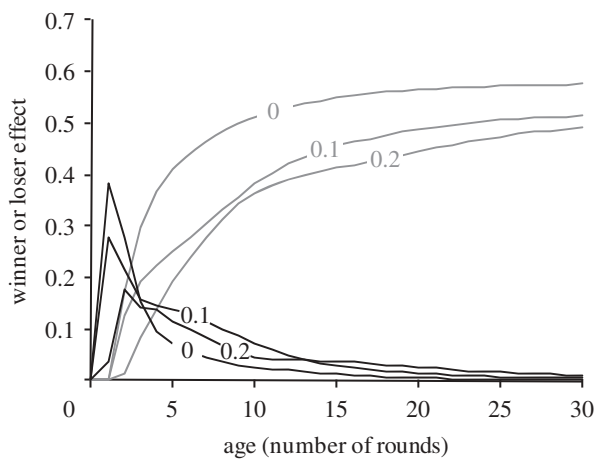
Figure 4. Age-dependent winner (grey) and loser (black) effects, calculated as the size of the increase (winner effect) or decrease (loser effect) in the average probability of playing Hawk for individuals that win or lose their next fight, respectively. The numbers on the lines indicate the chance (γ) that a weaker individual defeats a stronger individual in a fight. Other parameter values are given in the main text.

These effects are clearest when strong individuals have a big advantage (low γ), making the outcomes of fights more informative, but the age-related changes in winner and loser effects are a robust pattern (figure 4). Our model therefore makes the testable prediction that losing a fight should be a more powerful experience than winning for young individuals, in that it should lead to a more pronounced change in the tendency to escalate subsequent conflicts, whereas for older individuals the reverse should be true, with winning experiences having a bigger impact than losing.

4. DISCUSSION

When individuals are uncertain of their own fighting ability, they should adjust their level of aggression in response to their previous experiences in fights. Individuals winning many fights can afford to maintain a high level of aggression, whereas those suffering frequent defeats should adopt a non-aggressive strategy in which they withdraw when attacked. This confirms earlier theoretical work by Van Doorn *et al.* (2003*a*,*b*) showing that winner and loser effects are evolutionarily stable, and extends their conclusions to 'generalized' winner and loser effects in which there is no recall of specific opponents. These effects are analogous to adjustments in mate-choice rules according to the degree of interest received from potential mates (Fawcett & Bleay 2009), suggesting that sensitivity to previous experiences may be adaptive in a range of different contexts. The particular form of winner and loser effects shown in our model supports Hsu *et al.*'s (2006) interpretation that it is not an individual's actual fighting ability (which was fixed in our model), but their perception of this, that is modified by victory or defeat (Hsu & Wolf 2001; Hsu *et al.* 2009).

Uncertainty regarding one's own fighting ability generates some other interesting effects that give important insights into the evolution of aggressive behaviour. The opportunity to gather information to reduce this uncertainty means that engaging in fights can carry a fitness

benefit, separate from any resources that may be won or lost. These fitness benefits will be greatest for young, inexperienced individuals, who are unsure of their own strength and should therefore be willing to fight to test this. As they mature and gain experience, aggression should decline. Such a pattern has been well documented in humans by longitudinal studies examining the developmental trajectory of physical aggression (e.g. Tremblay *et al.* 1999; Tremblay 2000). For similar reasons, we expect high levels of aggression in naive individuals, such as those reared or kept for long periods in isolation and hence lacking in social experience. This has been observed in Siamese fighting fish (*Betta splendens*; Halperin *et al.* 1992, 1997) and black-headed gulls (*Larus ridibundus*; Groothuis & van Mulekom 1991). The latter study is particularly instructive, since the authors were able to pinpoint previous agonistic interactions as the necessary experience for a reduction in overt aggression. In general, early social experiences should be critical in enabling individuals to adopt an appropriate level of aggression in adulthood, as shown in experiments using laboratory mice (*Mus musculus*; Branchi *et al.* 2006) and rhesus macaques (*Macaca mulatta*; Stevens *et al.* 2009).

Our model also generates the novel, testable prediction that winner and loser effects should change with age and experience. Kahn (1951) showed that losing experiences in laboratory mice become less powerful with age, but few other studies of winner and loser effects have examined this possibility. Typically, researchers either disregard age differences between their subjects and differences in social experience prior to the experiment, or they select subjects of the same age and attempt to standardize prior experience through social isolation (reviewed in Hsu *et al.* 2006). Our model suggests that the strength of winner and loser effects in animals recently caught from the wild (e.g. Chase *et al.* 1994) are likely to differ from those in animals reared under standardized laboratory conditions with minimal social experience (e.g. Hsu & Wolf 1999). Where social isolation is used, subjects are often isolated shortly after birth (e.g. Bakker & Sevenster 1983; Whitehouse 1997; Hsu & Wolf 1999, 2001) or isolated for long periods of time (e.g. Ginsburg & Allee 1942; Schuett 1997). If our interpretation is correct, these approaches fail to detect important patterns of variation in how individuals respond to experiences of victory and defeat. Several studies find a strong loser effect but little or no winner effect (e.g. Francis 1983; Schuett 1997), with a meta-analysis by Rutte *et al.* (2006) suggesting that, averaging across studies, winners are twice as likely to win again, whereas losers are five times more likely to lose. Given the heavy reliance on young or socially inexperienced subjects, we do not find this surprising: these are precisely the individuals for which we would predict that loser effects are much stronger than winner effects. Tests using older, more experienced subjects may well reveal a different pattern. We urge empiricists to explore this possibility systematically by quantifying winner and loser effects in subjects of different age cohorts.

Our model could be extended in a number of interesting directions. One obvious area for future work is to alter the way we modelled strength. We assumed that individuals had a fixed strength throughout their lives, but in

reality this is likely to change with age. Incorporating detailed information on developmental trajectories and patterns of ageing would enable us to obtain more precise predictions regarding age-related changes in aggression and winner and loser effects. For example, we might expect that uncertainty about individual fighting ability, and hence aggression, would peak after periods of rapid growth (such as, for instance, the annual regeneration of antlers in deer). In addition, strength may change as a result of previous fights. Individuals that fight frequently are likely to deplete their energy reserves or incur injuries, perhaps particularly so when they lose. In severe cases, these costs may even increase the risk of death, in contrast to the fixed mortality rate (d) we assumed here for the sake of simplicity. We would expect non-aggressive behaviour to be more prevalent under these more dangerous conditions. Another change we could make is to allow a continuous distribution of strength, rather than the strong/weak dichotomy we considered here. However, previous theoretical work has shown that selection then favours a switch from non-aggressive to aggressive behaviour above a certain threshold strength (Crowley 2000; McNamara & Houston 2005), so we do not expect this would change our conclusions substantially.

A further assumption we made was that individuals encountered one another at random, such that old, experienced individuals would often be fighting against younger individuals who possess little information about their own strength. In many species, however, it is likely that contests are to some extent age-structured, with individuals competing primarily against others of similar age and experience. We expect that this would accentuate the age-related decline in aggression we have reported here, since escalation to a full physical fight should be most likely when both opponents are naive and least likely when both are well informed on their own strength. Further models are needed to explore these effects properly.

Memory of fighting experiences in real animals is unlikely to be encoded in exactly the same way as in our model, with a simple tally of the number of wins and losses. For example, recent experiences may often be weighted more strongly than older experiences (Hsu & Wolf 1999), particularly if fighting ability is variable and heavily influenced by changes in condition. In such situations, the sequence of victories and defeats may matter, rather than just the numbers of each. Our aim here was to illustrate the principle that responding to social experiences can be adaptive, so we focused on a simplified situation in which strength was fixed and therefore old experiences and recent experiences were equally informative. However, we expect that sensitivity to previous fight outcomes will be especially important when strength varies in an unpredictable manner, perhaps even favouring a certain rate of forgetting if old experiences give an outdated and unreliable indication of current state. An interesting challenge for the future is to investigate exactly what kind of information should be remembered under such conditions and how this might influence the form of aggressive behaviour.

In conclusion, we have shown that uncertainty over one's own strength generates a number of important effects, including winner and loser effects, information benefits from fighting and age-dependent changes in aggression. We suggest that the role of such uncertainty in shaping behaviour has been underappreciated in previous studies of aggression.

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