Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes

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ABSTRACT

Experience in aggressive contests often affects behaviour during, and the outcome of, later contests. This review discusses evidence for, variations in, and consequences of such effects. Generally, prior winning experiences increase, and prior losing experiences decrease, the probability of winning in later contests, reflecting modifications of expected fighting ability. We examine differences in the methodologies used to study experience effects, and the relative importance and persistence of winning and losing experiences within and across taxa. We review the voluminous, but somewhat disconnected, literature on the neuroendocrine mechanisms that mediate experience effects. Most studies focus on only one of a number of possible mechanisms without providing a comprehensive view of how these mechanisms are integrated into overt behaviour. More carefully controlled work on the mechanisms underlying experience effects is needed before firm conclusions can be drawn.

Behavioural changes during contests that relate to prior experience fall into two general categories. Losing experiences decrease willingness to engage in a contest while winning experiences increase willingness to escalate a contest. As expected from the sequential assessment model of contest behaviour, experiences become less important to outcomes of contests that escalate to physical fighting.

A limited number of studies indicate that integration of multiple experiences can influence current contest behaviour. Details of multiple experience integration for any species are virtually unknown. We propose a simple additive model for this integration of multiple experiences into an individual's expected fighting ability. The model accounts for different magnitudes of experience effects and the possible decline in experience effects over time.

Predicting contest outcomes based on prior experiences requires an algorithm that translates experience differences into contest outcomes. We propose two general types of model, one based solely on individual differences in integrated multiple experiences and the other based on the probability contests reach the escalated phase. The difference models include four algorithms reflecting possible decision rules that convert the perceived fighting abilities of two rivals into their probabilities of winning. The second type of algorithm focuses on how experience influences the probability that a subsequent contest will escalate and the fact that escalated contests may not be influenced by prior experience. Neither type of algorithm has been systematically investigated.

Finally, we review models for the formation of dominance hierarchies that assume that prior experience influences contest outcome. Numerous models have reached varied conclusions depending on which factors examined in this review are included. We know relatively little about the importance of and variation in experience effects in nature and how they influence the dynamics of aggressive interactions in social groups and random assemblages of individuals. Researchers should be very active in this area in the next decade. The role of experience must be integrated with other influences on contest outcome, such as prior residency, to arrive at a more complete picture of variations in contest outcomes. We expect that this integrated view will be important in

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understanding other types of interactions between individuals, such as mating and predator-prey interactions, that also are affected significantly by prior experiences.

Key words: animal contests, fighting experience, winner effect, loser effect, dominance hierarchy, observer effect, physiology, experience integration, predicting contest outcomes.

CONTENTS

I. INTRODUCTION

(1) Objectives

Careful observation of animals in nature reveals considerable variation within and among individuals in various types of behaviour (e.g. mating, foraging, aggression). Behavioural ecologists attempt to understand this variation by examining how the costs and benefits of fitness-related behaviour differ among individuals and environmental conditions. The obvious success of this costs and benefits approach (e.g. Krebs & Davies, 1997) leads us to take a similar approach to understanding the role of prior contest experience in aggressive interactions among individuals.

Early benefit/cost models of behaviour (e.g. marginal value theorem model of how long to remain foraging in a patch; Charnov, 1976) assumed that individuals had perfect information about the costs and benefits of alternative behavioural options. These omniscient individuals, while useful for developing first-generation models of behavioural variation, quickly were recognized as inappropriate caricatures in most circumstances. Naive individuals may not have perfect knowledge of either potential costs or benefits and their experience could change their perception, often toward reducing the differences between perception and reality. The degree to which the perception of costs and benefits by an individual approaches reality in any particular situation, however, will vary among individuals depending both on how fast the situation changes and on the influence of their prior experiences. The actual behaviour of an individual at any time may vary with the amount of information integrated from prior

experiences and its importance in determining current behaviour.

Experience influences the current behaviour of an individual, but how that translates into changed outcomes of the behaviour depends on whether the individual acts alone or in the context of other individuals. For solitary foraging individuals, modified expectations of costs and benefits usually can be assumed to translate directly into the choice among alternative foraging options. A solitary forager using a maximizing rule would be expected to visit the better of two patches, where better is defined in terms of the current expectations of costs and benefits of foraging in each patch (Kacelnik, Krebs & Ens, 1987). For individuals in aggressive interactions, or contests, the situation is more complex. The outcome of a contest presumably depends on the benefit and cost expectations of both participants, which often have been modified independently by prior experiences. The behaviour of each individual to some extent should be predictable based on their past experience, but the outcome of a contest will depend on how the experiences of each individual influence contest dynamics. Translation of prior experiences into changed contest outcomes is the subject of this review.

(2) Animal contests

Behavioural ecological models of contest behaviour and outcomes include assumptions about the level of information a contestant has about the costs and benefits of possible behavioural options in the contest. Individuals often compete directly with each other over access to limited resources such as mates (e.g. Austad, 1983; Crespi, 1986; Dickinson, 1992), breeding sites (e.g. Eckert & Weatherhead, 1987), food (e.g. Ewald & Carpenter, 1978; Riechert, 1986; Smith, 1990; Armstrong, 1991; Chapman & Kramer, 1996), and shelter (e.g. Dowds & Elwood, 1985). Fighting also is potentially costly to the contestants. The likely costs of fighting include (1) time and energy that otherwise could be allocated to other activities, e.g. search for alternative resources (Haller & Wittenberger, 1988; Haller, 1991; Thorpe, Taylor & Huntingford, 1995; Halperin *et al.*, 1998; Neat, Taylor & Huntingford, 1998); (2) physical injuries (Austad, 1983; Gottfried, Andrews & Haug, 1985; Robertson, 1986; McPeek & Crowley, 1987; Crowley, Gillett & Lawton, 1988; Marler & Moore, 1988; Neat *et al.*, 1998); and (3) greater risk of predation because individuals involved in physical fights may be less vigilant and/or more conspicuous (Jakobsson, Brick & Kullberg, 1995; Brick, 1999). Individuals are expected to integrate the potential costs and benefits associated with a contest and adjust their behaviour accordingly (Maynard Smith & Price, 1973; Maynard Smith, 1974; Maynard Smith & Parker, 1976).

Different hypotheses have been proposed for how costs (*C*) and benefits (*B*) should affect the outcomes of contests (e.g. Maynard Smith & Price, 1973; Maynard Smith, 1974; Maynard Smith & Parker, 1976; also see references below). The fighting strategies available to the contestants in these models could be discrete (e.g. Hawk and Dove game) or continuous (e.g. war of attrition). The contests that we are examining are better viewed as types of wars of attrition

where the outcome of a contest is determined by how long each contestant is willing to participate without retreating. The evolutionarily stable outcome is for the individual with lower *B/C* to retreat first (Hammerstein & Parker, 1982). When the increasing costs of continuing in the contest exceed the expected benefit an individual should withdraw to reduce further accumulation of costs in a contest that it will not win.

There are different ways that contestants may use information regarding *B/C* to settle conflicts. A group of models is built on the common assumption that rivals evaluate each other's *B/C* during contests and make fighting decisions based on their relative *B/C* (assessment models). These models differ in the types of information contestants acquired during contests. The *sequential assessment model* assumes that repeated interactions during a contest give the opponents information about the direction of the inequality in relative fighting abilities and that this information becomes more reliable as the contest proceeds (Enquist & Leimar, 1983; Enquist *et al.*, 1990; Briffa & Elwood, 2001). The *best-so-far rule model* and the *cumulative assessment model* propose that the contest is settled based on assessment of the action of greatest magnitude so far or the sum of the opponent's actions, respectively (Payne & Pagel, 1997; Payne, 1998). These models explain the fighting behaviour of some species that do not fit nicely within the sequential assessment model, particularly for situations in which actual physical contact may cause significant costs to the participants (see examples cited in Payne, 1998; Earley, Attum & Eason, 2002).

Different from the assessment models, the non-assessment model assumes that an individual's own *B* and *C* determine the time it will persist in a contest (Mesterton-Gibbons, Marden & Dugatkin, 1996; Payne & Pagel, 1997; Payne, 1998). An individual should retreat when its own *B/C* reaches a critical threshold. No information about the *B* and *C* of one's opponent is necessary, only how one's own *B* and *C* change during the contest (see examples in Mesterton-Gibbons *et al.*, 1996). In practice, it may be difficult to discriminate assessment from non-assessment explanations based on contest outcomes (Taylor & Elwood, 2003). Also, contestants are not confined to using one means of assessment; fiddler crabs (*Uca pugilator*) appear to follow sequential assessment rules in non-escalated contests but cumulative assessment rules during escalated contests (Pratt, McLain & Lathrop, 2003).

For these models to portray correctly or predict fighting decisions, contestants are expected to possess the ability to track changes in the costs and benefits associated with a contest. And, studies that manipulated resource values and/or fighting costs for contestants often successfully altered the contestants' behaviour as predicted. Generally speaking, contestants that expected a higher payoff tended to prolong the contest and/or escalate, and had a higher probability of winning (e.g. Riechert, 1979; Barnard & Brown, 1982; Austad, 1983; Leimar & Enquist, 1984; Dowds & Elwood, 1985; Ewald, 1985; Enquist & Leimar, 1987; Wells, 1988; Olsson, 1993). On the other hand, when potential fighting costs (e.g. probability of injury, energetically expensive behaviour) are increased as a result of

competing with larger opponents, individuals tend to retreat from a contest sooner (e.g. Barnard & Brown, 1982; Austad, 1983; Dugatkin & Ohlsen, 1990; Englund & Olsson, 1990; Enquist *et al.*, 1990; Dugatkin & Biederman, 1991; Polak, 1994; Stamps & Krishnan, 1994 *a*, *b*; Turner, 1994). Interestingly, larger contestants that should win based on relative fighting ability may opt not to fight, and appear to lose, if the current benefits are not sufficient (LeBoeuf & Peterson, 1969). These results provided empirical evidence that animals do monitor the costs and benefits associated with a contest and adjust their fighting behaviour accordingly.

(3) Utility of prior fighting experience

Experience could influence the perception of either costs or benefits and lead to variable outcomes of contests, even between the same two individuals, depending on the number, timing, and types of prior experience. Numerous observations (see Table 1), many discussed later, document such variable outcomes based on prior experience in contests. In general, losing decreases and winning increases the chance of winning a later contest (Table 1). Prior fighting experience should have influenced the fighting behaviour of contestants by affecting their assessment of the resource value or the costs associated with subsequent contests. It is possible that contest experience might provide information about potential benefits (Kennedy & Gray, 1994; but see Koops & Abrahams, 2003) and contest behaviour might indicate something about the quality of a mate or territory (Riechert, 1979; Austad, 1983; Brown & Gordon, 2000). However, for prior fighting experience to affect an individual's perception of resource value and cause the observed winner and loser effects, a winning experience would have to raise and a losing experience would have to lower the perceived value of a resource for an individual in future contests. It is not clear why winning and losing experience should have such effects on perceived resource values.

Winner and loser effects usually are hypothesized to result from prior winning and losing experience influencing an individual's assessment of its own fighting ability and estimated fighting costs in later contests (e.g. Parker, 1974; Beacham, 1988; Beaugrand, Goulet & Payette, 1991; Miklósi, Haller & Csanyi, 1997; Whitehouse, 1997; Hsu & Wolf, 1999; Mesterton-Gibbons, 1999). For contests in which opponents do not assess each other's fighting ability, fighting outcomes should not be affected by the outcomes of an opponent's prior fighting experiences. This is not to say that individuals do not gain valuable information from their prior experiences. In the non-assessment model, although a contestant does not assess its opponent's fighting ability, it may learn to estimate better how long it can/should last in a contest from its prior fighting experiences.

Prior contest experiences can vary in the permanence and timing of their effects on perception of costs depending on their predictability and the rate of environmental change. Permanent effects of experience can result from evolutionary or ontogenetic changes. Timing of effects can vary from evolutionary and developmental changes felt long after the experience to effects exerted immediately following the experience. Some aspects of estimating costs of contest behaviour and outcomes, such as the ability to assess size or morphological differences (Table 2), may be 'hard-wired' or learned very early in development (Young, 2003).

Experience effects that are not coded in gene frequency changes, but result from physiological and/or morphological changes, can also be relatively long term (e.g. Dufty, Colbert & Moller, 2002; Stamps, 2003). Cross-generational maternal effects can bias the behaviour of offspring (e.g. Mousseau & Fox, 1998). Similarly, experiences in early development can have profound effects on the behaviour of individuals as adults (DeGhett, 1975; vom Saal, 1979; Houtsmuller & Slob, 1990; Drummond, Torres & Krishnan, 2003; Wommack & Delville, 2003). Developmental effects on later behaviour can also include the improvement in fighting ability with practice. For instance, small pumpkinseed sunfish (*Lepomis gibbosus*) that had participated in more prior contests than their larger opponents won more contests (Dugatkin & Ohlsen, 1990). Practice does not seem to be an important factor to the winner and loser effects observed in most studies (Table 1) because losers with prior practice tended to lose to naïve opponents that did not have recent fighting experiences (i.e. those without practice). Practice may complicate interpretation of some experimental results and must be considered as a possible explanation for some effects derived from prior experiences (Popp, 1988; Stamps & Krishnan, 1998; Kim & Zuk, 2000). Developmental effects and hard-wired changes in contest behaviour, which occur over multi-generational time-scales as a product of natural selection, are not the focus of this review.

This review examines the ability of individuals to respond in a shorter-term, reversible, non-genetic fashion to experiences. This ability, however, is itself the product of natural selection that favours behavioural plasticity in relation to expected costs of contests in many organisms (West-Eberhard, 1989). These shorter-term responses to prior contest experience can involve learning or other physiological mechanisms, such as variation in hormone titres or receptors for hormone signals.

The basic descriptive model for the translation of experience in prior contests to current or future interactions and their outcomes is illustrated in Fig. 1. This review considers several aspects of experience effects: (1) changes in the probability of winning after experiences and likely influences of experimental methodology on detecting these changes; (2) relationship between behavioural and physiological, often neuroendocrine, changes following experience; (3) conceptual models of integrating multiple experience effects for an individual; (4) decision rules for predicting contest outcome from prior fighting experiences of the two opponents; and, (5) experience effects on dominance hierarchies. We hope that separating the stages of experience effects will alleviate the confusion in the literature between experience effects on physiology and behaviour and the changed outcome of contests. The outcome of a contest obviously depends on how experiences influence the behaviour of both contestants and how they respond to each other during the contest.

Table 1. A sample of studies that have investigated the effects of winning and losing on future contest outcome and/or aggressive behaviour, arranged by animal groups and listed in alphabetical order by species name (when provided). Methodological details of these studies are provided, including sample size (N), pre-experimental (pre-exp) isolation, procedures used to create winners and losers (type – random selection: RS; self selection: SS), length of experience (exper.) training, and recovery period. The effect of experience on contest success against naïve animals (W>N, L<N) or individuals of opposite experience (W >L) is also given. Effects of experience on any other types of agonistic behaviour are reported. The longevity of the experience effect is reported in parentheses when available. (N/A, not applicable; W, winner; N, naïve; L, loser; d, days; penult, penultimate; mo, months.)

| | | *Experience procedure* | | | | *Experience effect on* | | | | |
| | | | | | | *Probability of winning* | | | | |
Study organism	N	Pre-exp isolation	Type	Length of exper.	Recovery period	W>N	L<N	W>L	*Other behaviour*	Reference
Insects:										
Cricket[1] *Gryllus bimaculatus*	4	None	RS	67 min–few h	0 h			Yes		Alexander (1961)
Cricket *Gryllus bimaculatus*	16	>6 d	N/A	20 d group interaction	N/A				Significant runs of W/L. W-effect: increased probability of initiating	Simmons (1986)
Cricket *Gryllus bimaculatus*	120	6 h	SS	Variable	1, 5, 10, 20 min, 1 h, or 1 d	Yes ($\sim$10 min)	Yes ($\sim$10 min)		W-effect: shorter attack latency; L-effect: decreased intensity score, increased submission	Adamo & Hoy (1995)
Cricket[2] *Gryllus bimaculatus*	20, 60	24 h	SS	1 h	0 h			Yes	L-effect: decrease in aggressive behaviour and probability of initiating	Khazraie & Campan (1999)
Cockroach[1] *Nauphoeta cinerea*	7–23	?	SS	1–18 d	6–120 h			Yes (>120 h)		Ewing & Ewing (1973)
Burying beetle *Nicrophorus humator*	21	?	RS	3–4 h/d×15 d	24 h			Yes		Otronen (1990)
Arachnids:										
Spider *Argyrodes antipodiana*	16	Life	RS	5 min, 12 ×	14–24 h			Yes		Whitehouse (1997)
Crab spider *Misumenoides formosipes*	14	From penult. instar	RS	⩽1 h	1–10 d (mean = 4 d)			Yes		Dodson & Schwaab (2001)
Crab spider *Misumenoides formosipes*	35	From penult. instar	SS	⩽1 h	<72 h			Yes		Hoefler (2002)
Crustaceans:										
Swimming crab[3] *Necora puber*	15	>7 d	SS	0 h	0 or 2 h	No			Probability of initiation: W=N	Thorpe *et al.* (1995)

Table 1 (*cont.*)

Study organism	N	Experience procedure				Experience effect on			Other behaviour	Reference
		Pre-exp isolation	Type	Length of exper.	Recovery period	Probability of winning				
						W > N	L < N	W > L		
Crayfish *Orconectes rusticus*	30	⩾ 7 d	RS	5 min	20, 40, 60 min	Yes (< 60 min)			W-effect: does not increase likelihood of initiating at 20 min, but does at 40, 60 min	Bergman *et al.* (2003)
Crayfish[4] *Procambrus clarkii*	24	⩽ 14 d	SS	30 min × 2 for 3 d	> 6 h				W increase, L decrease % of fights won	Daws *et al.* (2002)
Fish: *Siamese fighting fish* Betta splendens	7	?	SS	30 min	?				Response rate toward mirror image: W > L	Baenninger (1970)
Siamese fighting fish *Betta splendens*	32	?	RS	15 min × 2 d × 4 sessions	24 h			Yes	W-effect: increase aggression toward mirror (relative to pre-experience); no change for losers	Wallen & Wojciechowski-Metzlar (1985)
Stickleback fish *Gasterosteus aculeatus*	5–42	Life	RS	15 min	0 h	Yes	Yes		Probability of roundabout fighting: N-N = W-W > L-W > L-L	Bakker & Sevenster (1983)
Stickleback fish *Gasterosteus aculeatus*	6–37	?	RS	15 min	0–6 h	Yes (< 3 h)	Yes (> 6 h)			Bakker *et al.* (1989)
Stickleback fish[5] *Gasterosteus aculeatus*	14	None	SS	30 min	4–5 h				No effects of W/L on behaviour toward territorial neighbour	Bolyard & Rowland (2000)
Green sunfish *Lepomis cyanellus*	17, 20	None	SS, RS	2 d, 5 d	0 h	No	Yes	Yes	Probability of initiation: W = N, L < N, W > L	McDonald *et al.* (1968)
Pumpkinseed sunfish *Lepomis gibbosus*	15, 18	4–8 d	SS	24 h	1.5 h	No	Yes	Yes		Beacham & Newman (1987)
Pumpkinseed sunfish[6] *Lepomis gibbosus*	4–12	5–6 d	SS	24 h	1.5 h			Yes		Beacham (1988)
Pumpkinseed sunfish *Lepomis gibbosus*	11–18	5–7 d	RS	0 h	0, 15, 60 min	Yes (< 1 h)				Chase *et al.* (1994)
Paradise fish *Macropodus opercularis*	20	1.5–2 mo	RS	24 h	1–28 d	No	Yes (< 7 d)		displays: no W/L effect; Decreased reactivity in L	Francis (1983)

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Paradise fish[7] *Macropodus opercularis*	24–60	3 d	SS	0 h–4 d	1–6 d				threatening, fighting, mouthlock & head-tail display (<6 d)	Miklósi *et al.* (1997)
African cichlid *Melanochromis auratus*	5	?	RS	Variable	?				Losing, not winning, affects hierarchy status; L-effect: decreased aggression; W-effect: increased aggression	Nelissen & Andries (1988)
African cichlid[8] *Pseudotropheus tropheops*	54	14–15 d	SS	Variable	0 h	No	Yes			Chase *et al.* (2003)
Mangrove rivulus[9] *Rivulus marmoratus*	27–38	Life	RS	1 h/exp × 2 exp	1 d	Yes (>2 d)	Yes (>2 d)	Yes (>2 d)	L-effect: decreased probability of initiation W-effect: increased probability of initiating with attacks, attacking first and escalating	Hsu & Wolf (1999, 2001)
Steelhead trout[10] *Salmo gairdneri*	10	24 h	SS	5–62 d	0 h			Yes		Abbott *et al.* (1985)
Blue gourami *Trichogaster trichopterus*	32	10 d	SS	24 h	0 h, 24 h	Yes	Yes		No W-effect, but strong L-effect: decreased initiation, decreased rates and duration of various aggressive acts	Frey & Miller (1972)
Green swordtail fish *Xiphophorus helleri*	7, 8	None	RS	24 h	0 h				Initiation of aggressive acts: W/N>L; W/N=L for latency to aggressive acts & dominance reversal	Thines & Heuts (1968)
Green swordtail fish[11] *Xiphophorus helleri*	34	18 h	SS	0 h	26 h			Yes	W increase and L decrease attack frequency toward mirror image	Franck & Ribowski (1987)
Green swordtail fish[12] *Xiphophorus helleri*	30	18–24 h	SS	Months				No	Display frequency: βmale > αmale	Franck & Ribowski (1989)
Green swordtail fish *Xiphophorus helleri*	12–43	2 h	SS	12 h	24 h			Yes		Beaugrand *et al.* (1991)
Green swordtail fish[13] *Xiphophorus helleri*	12–98	2 h	SS	12 h	24 h			Yes		Beaugrand *et al.* (1996)

Table 1 (*cont.*)

| Study organism | N | Experience procedure | | | | Experience effect on | | | Other behaviour | Reference |
| | | | | | | Probability of winning | | | | |
		Pre-exp isolation	Type	Length of exper.	Recovery period	W>N	L<N	W>L		
Green swordtail fish *Xiphophorus helleri*	20	3 h	SS, RS	18 h	3 h			Yes (SS)	RS>SS in: menace & attack frequency, aggression time	Beaugrand & Goulet (2000)
Green swordtail fish *Xiphophorus helleri*	59	64 h	SS	⩽1 h	0 h	No	No			Earley & Dugatkin (2002)
Reptiles: Copperhead snake *Agkistrodon contortrix*	10	6–12 mo	RS	15–20 min	1, 7 d	No	Yes (<7 d)		Probability of initiation: W=N, L<N (<7 d)	Schuett (1997)
Birds: Goldfinches[14] *Carduelis tristis*	12	None	SS	NA	NA				Significant increase in probability of winning after win for both dominants and subordinates; W-effect: increased probability of initiating & aggression	Popp (1988)
Domestic fowl[1] *Gallus domesticus*	8	None	RS	2–10 times × 5 min/d × 10 d	0 h				Rank in hierarchy decreased by losing	Ratner (1961)
Domestic fowl[1] *Gallus domesticus*	83, 37	None	RS	<24 h	2 h			Yes	L-effect: increased escape and freezing behaviour; W-effect: increased probability of initiating, increased frequency of aggression	Martin *et al.* (1997 *a*, *b*)
Blue-footed booby[15] *Sula nebouxii*	12	NA	SS	23–55 d	0 h			Yes		Drummond & Osorno (1992)
Blue-footed booby *Sula nebouxii*	22	NA	SS	14–21 d	>3 h	Yes (<6 d)	Yes (>20 d)		L-effect: increased submissive behaviour; W-effect: increased aggressive behaviour	Drummond & Canales (1998)
Mammals: Mice[1]	6,3	2 mo	RS	1–2 times/d × 8 d; 15 d; 16–42 d	<24 h	Yes	Yes			Ginsburg & Allee (1942)

Mice[16]	6–11	Life	RS	15 min/d × 3 d	30 d		L-effect: increased avoidance, defensive acts, squealing, nosing, jumping; decreased grooming, attacks	Kahn (1951)
Mice	72	?	RS	5 min/d × 7 d	>14 d		Readiness, persistence and intensity score: W>N, W>L	Bevan et al. (1960)
Mice	11	?	RS	10 min/2d × 4 times	2 d		W-effect: increased attack frequency, exploration, digging; decreased latency to attack, avoidance, threats	Martinez et al. (1994)
Rat	9–19	?	SS	0 h	1–11 d		L-effect: decreased aggressive-act frequency (>11 d)	Seward (1946)
Rat[17]	80	None	RS	30 min/d × 3 d	1 d, 14 d		W>L: time of aggression, autogrooming, activity & locomotion; L>W: approaching & mounting frequency	Van de Poll et al. (1982)
Syrian hamsters[18] Mesocricetus auratus	14, 18	14 d	RS	4 times × 5 min	24 h	Y (>16 d)	L-effect: decreased aggressive, increased submissive behaviour	Huhman et al. (2003)

[1] No statistical analysis provided.

[2] Post-experience pairs had engaged previously in group and dyadic settings; also examined effects of experience + isolation on dominance reversal.

[3] Individual with prior winning experience was transferred to the tank in which the naïve opponent had occupied for more than 24 h.

[4] Individuals fought 12 times prior to examining experience effects, with varying success; winner and loser effects cannot be assessed explicitly.

[5] Subjects community housed and transferred to test tank where they were exposed to neighbouring rival before experience testing.

[6] Prior losers needed to be at least 40 % larger than prior winners to have equal chance of winning.

[7] Individuals encountered the same opponents in the 1st and 2nd contests.

[8] In group contexts, winner effects remained not significant and the magnitude of loser effects diminished greatly; females used in this study.

[9] Examined the effects of both recent (1 d after) and penultimate experiences (2 d after).

[10] Discussed the relative importance between prior fighting experience and body size in determining the ability to dominate.

[11] In socially stabilized groups, high-ranking males attacked mirror image less frequently than low-ranking males.

[12] Only the results of highly escalated fights were reported.

[13] Discussed the relative importance of prior fighting experience, residency, and body size in determining the outcome of a contest.

[14] Study conducted on captive groups of birds; experience of opponent (e.g. N, W, L) was not determined but relative status between opponents was determined.

[15] Experience effects were greater than the effect of body size asymmetry.

[16] The effect of losing was more pronounced on younger individuals.

[17] Discussed the interaction between experience, testosterone, and sex effects on behaviours.

[18] Also tested females, which did not exhibit loser effect but did exhibit increased social behaviour toward non-aggressive intruder.

Table 2. Examples of characters that are correlated with fighting ability. Common name and specific character are given in parentheses if available.

| Organisms	References
Acoustic signals	
Cervus elaphus (red deer, roaring rate)	Clutton-Brock & Albon (1979)
Cervus elaphus (red deer, resonance frequencies)	Reby & McComb (2003)
Papio cynocephalus (baboon, calls)	Kitchen *et al.* (2003)
Saccopteryx bilineata (greater white-lined bat, song repertoire)	Davidson & Wilkinson (2004)
Trichopsis vittata (croaking gourami, sound characteristics)	Ladich (1998)
Body size (length/width/surface area)	
Acris crepitans blanchardi (Blanchard's cricket frog, body length)	Wagner (1989 *a*, *b*, 1992)
Anolis aeneus (lizard, body length)	Stamps & Krishnan (1994 *a*, *b*)
Archocentrus nigrofasciatum (convict cichlid)	Draud & Lynch (2002)
Arctopsyche ladogensis (net-spinning caddis larva, body width)	Englund & Olsson (1990)
Bufo bufo (toad, body length)	Davies & Halliday (1978)
Cichlasoma meeki (firemouth cichlid, body length)	Neil (1984)
Elaphrothrips tuberculatus (thrips, body length)	Crespi (1986)
Euophrys parvula (jumping spider, body width)	Wells (1988)
Exechesops leucopis	Kawashima (2004)
Frontinella pyramitela (bowl and doily spider, body length)	Austad (1983)
Gonodactylus bredini (stomatopod crustacean, body length)	Adams & Caldwell (1990)
Lacerta agili (sand lizard, body length)	Olsson (1992)
Metellina segmentata (autumn spider)	Hack *et al.* (1997)
Notophthalmus viridescens (red-spotted newt, body length)	Verrell (1986)
Oreochromis mossambicus (cichlid, body length)	Turner (1994)
Plexippus paykulli (jumping spider, distance between posterior-medial eyes)	Taylor *et al.* (2001)
Polistes fuscatus (paper wasp, head width)	Polak (1994)
Pomatoschistus minutus (sand goby, body length)	Lindstrom (1992)
Sorex araneus (shrew, body length)	Barnard & Brown (1982)
Xiphophorus helleri (green swordtail fish, lateral surface area)	Beaugrand *et al.* (1991)
Body mass (dry or wet)	
Acheta domesticus (crickets)	Hack (1997 *a*)
Agelenopsis aperta (desert spider)	Riechert (1984)
Agrypnia pagetana (caddisfly larvae)	Englund & Otto (1991)
Arctopsyche ladogensis (net-spinning caddis larva)	Englund & Olsson (1990)
Cervus elaphus (red deer)	Clutton-Brock *et al.* (1979)
Drosophila melanogaster (fruit flies)	Zamudio *et al.* (1995)
Euophrys parvula (jumping spiders)	Wells (1988)
Gallinula chloropus (moorhen)	Petrie (1988)
Lacerta agilis (sand lizard)	Olsson (1992)
Lepomis gibbosus (pumpkinseed sunfish)	Beacham (1988)
	Dugatkin & Ohlsen (1990)
	Dugatkin & Biederman (1991)
Nannacara anomala (cichlid fish)	Enquist *et al.* (1990)
Sorex araneus L. (shrew)	Barnard & Brown (1982)
Uperoleia rugosa (Australian frog)	Robertson (1986)
Cheliped size (weapon)	
Macrobrachium rosenbergii (prawn)	Barki *et al.* (1997)
Colouration/ plumage ornaments	
Gasterosteus aculeatus (three-spined sticklebacks, coloration)	Baube (1997)
Euplectes ardens (red-collared widowbird, Plumage ornaments)	Pryke *et al.* (2002)
Energy reserve	
Pagurus bernhardus (European hermit crab)	Briffa & Elwood (2004)
Fighting tactics	
Acheta domesticus (cricket)	Hack (1997 *a*)
Wing size	
LImenitis weidemeyerii (Weidemeyer's admiral butterfly)	Rosenberg & Enquist (1991)
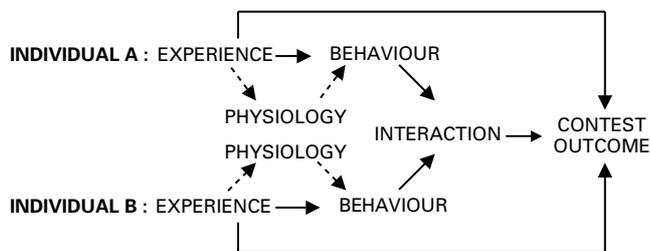
Fig. 1. Pathways for individuals A and B from contest experiences to modified contest outcomes based on those experiences. The dashed lines represent internal (i.e. physiological) changes that influence behaviour. The solid lines represent external events, including behaviour, a subsequent interaction, and the outcome of that interaction that are affected by the experience. We discuss each of these pathways in this review.

II. WINNER AND LOSER EFFECTS

(1) The role of prior fighting experience in animal contests

As discussed earlier [Section I (3)], prior fighting experience is usually hypothesized to affect a contestant's fighting behaviour by altering its estimated fighting ability. An individual may assess its fighting ability differently after a contest because its 'actual' fighting ability is truly altered by the contest outcome, i.e., prior wins increase while prior losses decrease actual fighting ability (Parker, 1974; Beacham, 1988; Beaugrand *et al.*, 1991). Parker (1974) proposed that experience altered resource holding power (RHP), consistent with the finding that winning experience increased the 'readiness' for escalation in mice and rats (Scott & Fredericson, 1951). The mechanisms of how winning/losing experience may alter the true fighting ability for an individual, however, have never been proposed. An alternative hypothesis to altering actual fighting ability is that outcomes of prior fights add to the information that an individual has for evaluating its own perceived fighting ability (Miklósi *et al.*, 1997; Whitehouse, 1997; Hsu & Wolf, 1999; Mesterton-Gibbons, 1999). In this case, winning experiences would raise and losing experiences would lower, an individual's perceived fighting ability and affect its anticipated fighting costs accordingly. Both hypotheses predict that prior fighting experiences would influence an individual's estimation of fighting costs and thus the probability of winning a subsequent contest.

The two hypotheses differ in their predictions about the importance of prior experience as contests progress from displays to intense physical fights. Direct physical interactions provide more reliable means for contestants to compare their true fighting ability than displays, and as a contest progresses to later stages with more costly physical interactions, more reliable information would have been accumulated. If prior experiences influence how an individual assesses its perceived fighting ability but do not change its actual fighting ability, prior experiences should have a significant impact on fighting behaviour in the early stages of a contest before physical interactions occur. Once a contest escalates to costly physical interactions, the contestants

are able to compare their actual fighting ability directly and the importance of the information from past experiences should subside. If prior experiences alter an individual's actual fighting ability, then they should influence fighting behaviour both before and during physical interactions.

In the mangrove rivulus (*Rivulus marmoratus*), previous fighting experiences had a significant influence on the outcomes of contests resolved without physical fights but not on those that escalated into physical fights (Hsu & Wolf, 2001). Male copperheads (*Agkistrodon contortrix*) with a prior winning experience won two out of the two non-escalated contests, but won only four out of the eight escalated contests (Schuett, 1997). In contests between size-matched male swordtails (*Xiphophorus helleri*) previous rank did not affect the probability of winning highly escalated fights (Franck & Ribowski, 1989) even though prior winning/losing experiences have a significant effect on the probability of winning a subsequent contest in this species (Beaugrand *et al.*, 1991; Beaugrand, Payette & Goulet, 1996). These results are consistent with the hypothesis that prior experiences influenced fighting behaviour by affecting how contestants assess their fighting abilities but do not support the hypothesis that the actual fighting ability of contestants was modified.

(2) Influence of methodology on detecting experience effects

Researchers studying experience effects on fighting behaviour often adopt different experimental procedures, which probably contribute to differences in their conclusions regarding winner and loser effects (Chase, Bartolomeo & Dugatkin, 1994; Beaugrand & Goulet, 2000). The first methodological difference is the protocol used to offer fighting experiences to focal individuals. The procedures can be grouped roughly into random-selection or self-selection (Chase *et al.*, 1994; Beaugrand & Goulet, 2000). In self-selection methods, two individuals are matched for size and allowed to fight. The winner and loser are treated as having a winning and losing experience, respectively. Although the self-selection procedure might appear to be a more 'natural' method for contestants to acquire experiences (Beaugrand *et al.*, 1991; Bégin, Beaugrand & Zayan, 1996), it could confound the apparent role of fighting experience with intrinsic fighting ability (Chase *et al.*, 1994; Bégin *et al.* 1996). For instance, Bégin *et al.* (1996) deduced that self-selected winners have a 0.67 probability of having intrinsically higher fighting ability than a size-matched naïve opponent in a second contest, as opposed to a 0.5 probability under random-selection conditions (see below) (Bégin *et al.*, 1996). Therefore, when the self-selected procedure is employed, experience effects should be evaluated with the appropriate null hypothesis that accounts for the probability of intrinsic differences among the subjects (i.e. testing against a null of 0.67 *in lieu* of 0.5).

Random selection procedures give pre-determined experiences separately to individuals that have been chosen at random for a later contest. Pitting focal individuals against habitual winners or large opponents creates pre-determined losers; pitting individuals against habitual losers or small opponents creates pre-determined winners. This method

attempts to randomize intrinsic differences between contestants to focus solely on the effects of the experience. We suggest that the randomly selected procedure should be used unless a strong argument can be made to the contrary in the context of a particular experiment.

The second methodological difference involves the frequency and duration of experience training, which vary from terminating the experience session immediately following contest settlement (Chase et al., 1994) to allowing the contestants to remain together for as long as 62 days (Abbott, Dunbrack & Orr, 1985). Time differences in experience training among studies may cause differences in energy depletion, bodily injury, physical exhaustion, and other physiological attributes in individuals that receive winning or losing experience. Naïve opponents do not go through experience training and are not subjected to these effects. Prolonged experience training could be a disadvantage for winners and losers when fighting against naïve opponents and thus could augment the effect of losing experiences but obscure the effect of winning experiences.

The influence of experience variation on fight outcome may not be trivial. Accidental deaths occurred in early studies of experience effects in green sunfish (Lepomis cyanellus; McDonald, Heimstra & Damkot, 1968) and male cockroaches (Nauphoeta cinerea; Moore, Ciccone & Breed, 1988). Leg injuries from experience training caused individuals of burying beetles (Nicrophorus humator; Otronen, 1990) to be removed from the study. Fin damage also was observed in studies of paradise fish (Macropodus opercularis; Francis, 1983) and steelhead trout (Salmo gairdneri; Abbott et al., 1985). These examples demonstrate that physical injuries can occur during experience training. The risk and severity of such injuries might increase with the length of experience training. Results regarding the magnitude and the extinction of experience effects from studies with lengthy experience training may be confounded by physical injuries experienced by the focal animals.

Duration and frequency of experiences could also influence the physiological response to experience. Changes in hormone titres associated with experience effects [see Section III (2)] may increase or decrease as the length of the experience increases. Wistar rats exposed to repeated 4 h aggressive encounters exhibit substantially higher corticosterone levels than animals exposed to repeated 30 min interactions (Zelena et al., 1999). Until further studies are conducted that compare physiological changes over time following termination of an experience, and changes with a continued experience, we cannot draw firm conclusions about the actual effect. A recent study in paradise fish (M. opercularis), however, concluded that duration of postcontest harassment had no significant influence on experience effects (Miklósi et al., 1997).

Experience effects can be detected when training is terminated as soon as winner/loser status is established (e.g. Seward, 1946; Franck & Ribowski, 1987; Chase et al., 1994), or after a relatively short period of time ($\leqslant 1$ h of interaction; Kahn, 1951; Bevan, Daves & Levy, 1960; Baenninger, 1970; Bakker & Sevenster, 1983; Bakker, Bruijn & Sevenster, 1989; Schuett, 1997; Whitehouse, 1997; Hsu & Wolf, 1999, 2001). Therefore, prolonged

experience training does not seem necessary to ensure delivery of experiences, and should be justified if employed.

A third methodological difference involves the amount of time focal individuals were allowed to recover from their experience before testing for the experience effects. Some studies tested immediately after experience training (e.g. Alexander, 1961; McDonald et al., 1968; Frey & Miller, 1972; Bakker & Sevenster, 1983; Abbott et al., 1985; Bakker et al., 1989; Chase et al., 1994; Thorpe et al., 1995) and others tested 2 or more days after experience (e.g. Kahn, 1951; Bevan et al., 1960; Martínez, Salvador & Simon, 1994). The time interval may have two influences on experience effects. Long time intervals provide focal individuals a chance to recover from the physical exhaustion/injury of experience training and replenish the energy consumed (if food is provided). However, if experience effects are transitory or decay with time (see Section IV), the length of the time interval may influence the likelihood of detecting the presence and/or magnitude of the experience effect (Chase et al., 1994).

The last methodological difference involves isolation of focal individuals before experience training. Some studies isolated focal individuals shortly after birth and thus controlled for fighting experience prior to their studies of experience effects (e.g. Kahn, 1951; Bakker & Sevenster, 1983; Whitehouse, 1997; Hsu & Wolf, 1999, 2001). Others did not isolate the focal individuals at birth but isolated them for relatively long periods of time before use (months, e.g. Ginsburg & Allee, 1942; Schuett, 1997) or justified their isolation intervals by providing evidence that the intervals were sufficient for most of the experience effects to disappear (e.g. Beacham, 1988; Chase et al., 1994; Earley & Dugatkin, 2002). Many investigators, however, were not careful to ensure that the effects of previous interactions disappeared before conducting new experiments or were not clear about whether they isolated their study subjects (Table 1). The experience effects measured in these studies might be influenced by unknown earlier experiences, including earlier experiences between the test pair that could introduce individual recognition as a contest cue [see Section VI (8)].

Several studies have noted that individuals reared in isolation have higher aggression levels than individuals reared together (e.g. Halperin, Dunham & Ye, 1992; Halperin & Dunham, 1993; Halperin, Giri & Dunham, 1997). Most investigations of experience effects, however, are not interested in absolute levels of aggressive behaviour. The effects of isolation should not influence fight outcome unless isolation produces naive individuals that are near or at the maximum possible aggressive level. In this case, a winning experience might have no effect in a contest with a naive individual. This was not the case in the studies using mangrove rivulus individuals reared in isolation from shortly after birth (Hsu & Wolf, 1999) although it is not known whether it is an important factor in experience investigations for other species.

When short-term isolation is used as a pre-treatment to minimize the effects of prior experience on focal contests, variable results have been obtained. A recent review by Gomez-Laplaza & Morgan (2000) revealed conflicting effects of social isolation on aggressive behaviour, with some

studies demonstrating increased and others decreased aggression levels following social isolation. Some of the inter- and intraspecific variation in response to social isolation can be attributed to the length of the isolation period, social system (e.g. territorial *versus* group-living), or developmental stage (e.g. juvenile *versus* adult; Gomez-Laplaza & Morgan, 2000). Considerable intraspecific variation (e.g. status- or age-dependent) in the aggressive response to social isolation could impact interpretations of how experience effects influence contest outcome, particularly if experienced animals are re-isolated before encountering a naïve opponent or if isolation has stimulatory or inhibitory effects on aggression in the naïve opponents.

Methodological differences among studies could have profound influences on the results of the studies examining experience effects. We urge researchers interested in experience effects to consider all of the factors described above when designing new studies. If possible, standardized procedures should be adopted to facilitate data comparison among different studies. In addition, systematic studies of the effects of each methodological difference, such as that carried out by Miklósi *et al.* (1997), would be useful.

(3) Relative importance of winner *versus* loser effects within species

The effects of experience on individual contest behaviour or contest outcome will depend on both the magnitude of the initial effect and whether that effect dissipates through time. Most studies report only how the probability of winning a contest changes following an experience. This probability may differ both with how the experience was provided and when the effect was measured. The most general outcome is for previous winners to have an increased and previous losers to have a decreased chance of winning.

In many species, the effect of a winning experience disappears sooner than the effect of a losing experience. For example, in sticklebacks the effect of a winning experience lasted for less than 3 h, but a losing experience effect persisted for more than 6 h (Bakker & Sevenster, 1983; Francis, 1983; Beacham & Newman, 1987; Bakker *et al.*, 1989; Chase *et al.*, 1994; Huhman *et al.*, 2003). One exception to this general trend is mangrove rivulus, in which winning and losing experiences had opposite but equal effects on the outcome of fights 24 and 48 h after the experiences (Hsu & Wolf, 1999).

Frequently observed differences in the longevity of winner and loser effects may be due to differences in the initial magnitude and/or rate of temporal decay of these effects. Unfortunately, information on the initial magnitudes and the decay rates of winner and loser effects is very limited because researchers do not always test for the effects right after completing the experience training (Table 1). Even when researchers tested for the effects immediately, they did not always test for the effects of winning and losing experiences separately by fighting the trained individuals against naive opponents. And, for the studies that examined winner and loser effects separately, their sample sizes were often satisfactory for drawing qualitative conclusions (i.e. whether or not winner/loser effects existed) but were inadequate for making quantitative statements about the magnitude of the effects (but see Bakker *et al.*, 1989).

Differences in the relative magnitude and longevity between winner and loser effects may not be random variation. The relative importance of the information from winning and losing experiences may have differential effects on the future fitness of an individual. One possible cause for the often greater and/or longer-lasting loser effect is that engaging in contests, but losing often incurs more costs (time, energy, injuries) than retreating without confrontation (Neat *et al.*, 1998). These high costs of losing could select for individuals that adopt more 'conservative' strategies such that their fighting behaviour is more likely to be modified by losing experiences than by winning experiences. Because different studies often employ different procedures to estimate fighting costs [Section III (2)] and to study experience effects, the information needed to examine the explicit relationship between fighting costs and the relative importance of winning and losing experiences is not currently available.

A more pronounced loser effect also may be a consequence of the fact that losers have more 'control' of the outcome of a contest (Mesterton-Gibbons, 1999). Individuals with prior losing experience often voluntarily retreat from a subsequent contest without physically interacting with their naïve opponents (e.g. Schuett, 1997). In contests with prior winners, however, naïve opponents are more likely to escalate the contest (e.g. Schuett, 1997; Hsu & Wolf, 1999). As discussed earlier, once a contest escalates, the value of information from past fighting experience is greatly diminished and contest outcome should be determined primarily by the intrinsic fighting ability of the two contestants. Therefore, if naïve individuals tend to escalate, the effect of winning experiences would be more difficult to detect by observing only contest outcomes.

If the effect of winning and losing experiences on estimated fighting ability is of similar magnitude, but opposite sign, an apparent asymmetry in their effects on fighting outcome could emerge if the probability of winning is a function of the relative difference between the estimated fighting ability of the two opponents [Section V; Equation (3)]. Assume a group of similar-sized naïve individuals all with initial perceived fighting ability of 15, and that experience changes the estimation of ability by 5 units. Then allow each experienced individual to fight against a similar-sized, naive opponent. The probability of winning for the previous winner would be $(15+5)/[(15+5)+15]=0.57$ (an increase of 0.07 from its probability when naive) while the probability for the previous loser would change to $(15-5)/[(15-5)+15]=0.40$ (a change of 0.10 from its probability when naïve). As the effect of the experience increases the difference between the change for a winner and loser also increases. If the effect of experience is 12 units, then a previous winner experiences a $+0.14$ (0.64) probability of winning against its new naive opponent, while a loser experiences a -0.33 (0.17) change from its naive state (0.5). Such asymmetric experience effects would not appear if the probability of winning is a function of the absolute difference between the estimated fighting ability of the two opponents [Section V; Equation (2)]. Thus, the 'rule' for

predicting contest outcomes from integrated experiences must be known to test for differences in experience effects [see Section V].

(4) Interspecific differences in experience effects

The relative importance of winner *versus* loser effects, and how long each effect persists also seems to vary among species [see examples in Section II (3)]. The value of the information obtained through winning and losing experiences depends on its reliability. Any factors that influence the reliability of information from a previous fight are likely to influence how long the effect lasts. For example, if relative size of contestants is an important determinant of fight costs, individuals of a species that grows fast may retain information from a previous fighting experience for less time than individuals of a species that grows more slowly. Within a population, an individual that is at its peak growth rate might be expected to retain information from a previous fight for a shorter period than an individual that is no longer growing. Similarly, for individuals with indeterminate growth (e.g. fish; Patnaik, Mahapatro & Jena, 1994), experience effects might remain transitory for life. Moreover, if an individual's fighting ability fluctuates greatly over time, for example, if ability is influenced by its energy reserve which depends on the food intake shortly before a contest, the outcome of previous fights would provide very little value to predicting the outcome of future fights (Mesterton-Gibbons & Dugatkin, 1995).

How long the information from an experience remains useful to an individual also may be related to the frequency of social encounters (Schuett, 1997). In a population where aggressive encounters occur at high frequency, individuals more often obtain recent and hence potentially more reliable information. It is thus less useful to preserve information from past aggressive interactions. By contrast, when social interactions occur rarely but the information remains reliable for a long time, it would be adaptive to retain the information longer. The longevity of experience effects in male copperheads (loser effect > seven days; Schuett, 1997) and sticklebacks (loser effect < 24 h; Bakker *et al.*, 1989) matches their social structures. In their natural environment, social interactions between male copperheads are infrequent (Schuett, 1997). Sticklebacks, however, live in groups for a majority of the year (except when males establish breeding territories) where social interactions can occur frequently (Wootton, 1976; Rowland, 1989). It is thus reasonable for experience effects to be more transitory in sticklebacks than in copperheads.

(5) Quality of experience effects

We have been discussing fighting experience as if it did not vary with the quality of a specific experience. The magnitude of the effect of either a win or a loss could be influenced by variation in the characteristics of specific winning or losing experiences. For example, a win or loss against an opponent of different size might yield changes to the assessment of one's fighting ability that are different from a win or loss against a similar-sized opponent (Beaugrand &

Goulet, 2000). A low-quality opponent that is easy to beat may give an individual less information about its own fighting ability than a high-quality opponent that is difficult to beat. Thus, the effect of wins and losses may differ in magnitude with the 'quality' of either type of experience. Although the hypothesis that the magnitude of an experience effect, in terms of winning probability, may vary with its 'quality' remains untested, some evidence suggests that the intensity of a prior conflict differentially affects subsequent aggression levels in winners (Goulet & Beaugrand, unpublished data).

(6) The importance of experience effects in fighting decisions and outcomes

Many factors interact to determine the behaviour of contestants and the outcome of a contest. Experience is only one of these influences and must be integrated with the other intrinsic (e.g. size, weaponry, condition; Table 2) and extrinsic (e.g. residency, social context) factors to predict final outcome. These factors all potentially influence the B/C for each contestant and can modulate the role of prior experience in determining the interaction between behaviour and outcome.

The reliability of these indicators of fighting ability in predicting the outcome of a contest increases as asymmetries between contestants increase. Also, as the reliability and importance of other cues increases, the usefulness of prior experience should decrease, and *vice versa*. Relatively little is known about how specific indicators scale in this trade-off with experience. A few studies examined the importance of prior fighting experience relative to other indicators of fighting ability, especially size differences, in predicting the outcome of a contest (e.g. Abbott *et al.*, 1985; Beacham, 1988; Beaugrand *et al.*, 1991, 1996; Drummond & Osorno, 1992; Carpenter, 1995; Zucker & Murray, 1996; Schuett, 1997; Cloutier & Newberry, 2000; Hoefler, 2002).

In steelhead trout a 5 % difference in body mass usually assured dominance for the larger fish but, subordinates failed to win against opponents with winning experience even after the subordinates were provided with extra food and outweighed the opponent by 62–114 % (Abbott *et al.*, 1985). However, physical injuries stemming from a lengthy interaction period (50–60 days) and individual recognition might have contributed to the subordinates' inability to reverse the dominance relationship, confounding the role of prior experience effects [Section II (2)]. Using random selection procedures, male copperheads that received a losing experience through fighting with bigger opponents lost subsequent fights to naïve individuals that were 8–10 % smaller in snout-vent length (Schuett, 1997). Because 8–10 % differences in snout-vent length between naïve contestants ensured 100 % probability of winning for the larger individuals, this result indicated that prior losing experience was more important in determining the fighting outcome in male copperheads when body size difference was less than 10 %. Only one size difference was investigated in the study and it is not clear whether the importance of prior losing experience would decrease as the body size difference increases.

In pumpkinseed sunfish and green swordtails (Beacham, 1988; Beaugrand *et al.*, 1991), contest outcome was determined primarily by the prior contest history of the two contestants when size differences between them were small (<40% in body mass for pumpkinseed sunfish, <25 mm^2 in lateral surface area in green swordtail). As size differences increased (>80% in pumpkinseed sunfish, >150 mm^2 in green swordtail), the tendency for the bigger opponents to win the contest increased and the influence of prior experience became negligible. Beaugrand *et al.* (1996) examined the relative contribution of asymmetries in prior experience, size, and prior residency of 3 h to fight outcome in green swordtails. When differences in lateral surface area exceeded 20%, body size uniquely determined outcome and nullified asymmetries in prior fighting experience and residency. When the size difference was between 10 and 20%, both size and prior fighting experience affected fighting outcome. Prior residency of 3 h was an advantage only when both opponents had prior losing experience and the size difference was small (<20%). Caution should be exercised when interpreting these results because the focal individuals in these studies received winning and losing experiences through a self-selection procedure [see Section II (2)].

The results of these studies have illustrated that the importance of experience effect on contest outcome is negatively influenced by the body size difference between the two contestants. Because it is difficult to control and quantify the effects of prior fighting experience, no studies have examined whether a larger difference in fighting experience could diminish the effects of a larger difference in body size (or other fighting-ability variable) between two contestants. Moreover, asymmetries in resource value, prior residency (Beaugrand *et al.*, 1996), energy reserves (Marden & Waage, 1990), and other factors that influence contest costs (e.g. predation) also should have an impact on the importance of experience effects and should be considered in predicting the outcome of a contest. Ultimately the complex interaction of relative magnitudes of difference in all factors that influence contest behaviour will need to be integrated to predict contest outcome accurately.

(7) Observer effects

Experience that does not involve actual participation in a contest may provide important information about possible success in a subsequent contest. Eavesdropping refers to a phenomenon where bystanders extract information from aggressive contests between others and update their perception of the fighting abilities of these individuals based on the dynamics and/or outcome of the witnessed contest (McGregor & Dabelsteen, 1996; see Brown & Laland, 2003 for a brief review). When the risks of fighting are especially high, eavesdropping may be a more cost-effective assessment strategy than engaging in actual physical combat, particularly for group-living animals (Johnstone, 2001; Nakamura & Sasaki, 2003). Several recent studies in birds and fishes provide evidence that information extracted from contests between others influences an individual's decision to interact aggressively with previously monitored

conspecifics (McGregor, Dabelsteen & Holland, 1997; Naguib & Todt, 1997; Oliveira, McGregor & Latruffe, 1998; Naguib, Fitchel & Todt, 1999; McGregor, Peake & Lampe, 2001; Peake *et al.*, 2001; Earley & Dugatkin, 2002). For instance, male green swordtails that observed a contest avoided initiating aggression against both winners and eventual losers that persisted in the watched interaction (Earley & Dugatkin, 2002). Furthermore, integrating prior experiences with the information gained by watching fights can increase the reliability of assessment *via* observation (Peake *et al.*, 2002).

Watching fights also triggers physiological changes. Tilapia (*Oreochromis mossambicus*) experience elevated levels of 11-ketotestosterone after viewing an aggressive interaction between two conspecific males (Oliveira *et al.*, 2001). Given the potential association between androgen levels and aggressive behaviour [see Section IV], Oliveira *et al.*'s (2001) data suggest that watching fights might increase the observer's success in future encounters, even with unfamiliar opponents. To test the idea that watching fights elicits general changes in aggressive motivation, Earley, Druen & Dugatkin (2005) exposed green swordtail males to fights and then assessed the observers' response toward naïve conspecifics (i.e. inexperienced individuals that were not observed). Individuals that watched fights responded similarly toward the naïve animals as those that had not been exposed to a fight. Clotfelter & Paolino (2003), however, demonstrated that individuals of Siamese fighting fish (*Betta splendens*) that had watched a fight experienced heightened aggression levels and increased probabilities of winning against naïve opponents. Differences in the response of swordtails and fighting fish to viewing aggressive contests suggests that such 'priming' effects may be taxon specific. Studies that simultaneously examine observation-induced changes in steroid hormone levels and agonistic behaviour have yet to be conducted. Such studies will provide a more complete picture of how experience obtained by watching fights influences subsequent behaviour and contest success.

III. MECHANISMS OF EXPERIENCE EFFECTS

An individual's previous agonistic interactions must induce some physiological changes that modify behaviour in order to influence the outcome of its current contest. We first discuss how experience influences behaviour, and then consider possible physiological and neuroendocrine modulation of these behavioural changes.

(1) Experience effects on fighting behaviours

If fighting experiences modify an individual's estimate of its fighting ability, individuals with winning (losing) experience should initially behave as if they have better (worse) fighting ability than a size-matched naïve opponent. When contests progress to later stages the effect of prior fighting experience should decrease [see Section II (1)].

The most commonly examined behavioural change after a previous contest is the probability of initiating future

contests. In green sunfish (McDonald *et al.*, 1968), green swordtails (*Xiphophorus helleri*) (Thines & Heuts, 1968), and dark-eyed juncos (*Junco hyemalis*) (Jackson, 1991), prior winners were more likely to initiate future confrontations than prior losers. In the dark-eyed junco, however, the influence of prior winning experience on the probability of initiation disappeared after considering the effects of sex, wing length, and hood colour. When the effects of a winning or losing experience on the likelihood of initiation are examined separately, the negative effect of losing usually remains significant, while the effect of winning becomes undetectable (e.g. McDonald *et al.*, 1968; Frey & Miller, 1972; Schuett, 1997; Hsu & Wolf, 2001).

Many features of fighting behaviour other than the likelihood of initiating aggressive encounters are influenced by fighting experience. Individuals with winning experience generally are more active/responsive (Baenninger, 1970; Van de Poll *et al.*, 1982) and aggressive (Van de Poll *et al.*, 1982; Martínez *et al.*, 1994) than individuals with losing experience. Winning experiences increased the readiness and intensity of competitive behaviour in mice (Bevan *et al.*, 1960), the frequency of initial attacks on a mirror image in swordtail fish, although this effect reversed over time (Franck & Ribowski, 1987), and the frequency and persistence of territorial behaviour in blue gouramis (*Trichogatster trichopterus*) (Hollis *et al.*, 1995). In mangrove rivulus, prior winning experiences increased the probability of starting a confrontation with physical attacks, the probability of launching the first attack, and the likelihood of escalating into physical fights (Hsu & Wolf, 2001).

Evidence of loser effects on behaviour in contests is more abundant (and consistent) than evidence of winner effects. A losing experience decreased the frequency/duration of aggressive acts (e.g. attack, chase, etc.) in rodents (Seward, 1946; Kahn, 1951) and fishes (Frey & Miller, 1972; Bakker & Sevenster, 1983; Franck & Ribowski, 1987). Losing experiences also decreased movement in paradise fish (Francis, 1983), and increased the avoidance and/or defensive behaviours in mice (Kahn, 1951) and male copperhead snakes (Schuett, 1997).

To summarise, an individual usually becomes more passive and cautious after a losing experience. Although no clear evidence indicates that a prior winning experience influences the likelihood of initiating a contest, it generally increases the activity level and the readiness of an individual to adopt more costly behaviour.

The next question is how changes in fighting behaviour eventually influence fighting outcomes. Studies that examined experience effects on behaviour did not always examine fighting outcomes, and *vice versa*. Therefore, this information is only available for a handful of species. In male copperhead snakes, individuals with a prior losing experience never initiated any confrontation and avoided physical fights by retreating immediately when challenged by naïve opponents and thus, lost all their fights (Schuett, 1997). Prior winning experience did not have a significant effect on the probability of initiating or winning a contest in male copperheads. In mangrove rivulus, a substantial proportion (39%) of prior losers retreated immediately when challenged, and losers rarely initiated the confrontation.

An individual that attacks its opponent at the outset usually wins, with the retreat rate of opponents being 94% in mangrove rivulus. Only 59 of 153 staged contests were initiated with attacks and the likelihood of attack was influenced by an individual's fighting experience; prior winners, but not prior losers, often initiate with attack (Hsu & Wolf, 2001). By increasing the likelihood of initiating with attacks, winning experiences increased the probability of an individual deterring its opponent. These results indicate that early in a contest individuals signalled honestly in relation to their prior experience. However, it is not clear what prevents individuals of mangrove rivulus from cheating with a dishonest signal early a contest. Perhaps this relates to the risk of retaliation. Winning experiences consistently increased the probability of retaliation in mangrove rivulus and eventually increased the probability of escalating a confrontation into a physical fight. This further decreased the chance that an individual with winning experience would retreat without obtaining a more accurate assessment of its relative fighting ability. Because prior winners tend to escalate, opponents will not benefit from cheating with a dishonest signal early in a contest (see Earley, Tinsley & Dugatkin, 2003; Just & Morris, 2003; Moretz, 2003 for alternative explanations on why likely losers would initiate fights).

(2) Experience effects on physiology

Short-term changes in behaviour and ultimately in contest outcomes resulting from prior experiences are likely to result from two somewhat different, but overlapping physiological mechanisms – learning and neuroendocrine. The changes in either case are associated with the effects of experience on the neuroendocrine system of the individual.

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

Contest behaviour is also modified as a result of learning. Classical dominance hierarchies may depend on learning the identity of particular individuals and responding as if the expectations of costs have shifted as a result of prior experience in contests or watching contests (e.g. Oliveira *et al.*, 1998; Dugatkin, 2001). Pavlovian conditioning has been used to change the behaviour of a resident blue gourami to anticipate a fight with a potential intruder (e.g. Hollis, 1984; Hollis *et al.*, 1995). Following presentation of a light cue that was earlier paired with the appearance of the intruder, the resident moved out to confront the potential intruder and engaged in early stages of contest signalling in the absence of an intruder. In this case, learning changed the behaviour of the resident in a way that could reduce costs and increases its chances of winning the potential fight through early engagement of an intruder.

Learning itself is reflected in physiological changes in synaptic transmission rates in specific neuronal pathways. Whether these are changes in postsynaptic response to neurotransmitters or to the release or regulation of levels of neurotransmitters is not critical to the discussion here, merely that learning results from physiological change. Learning and forgetting rates then would be associated with how the experiences influence these changes in synaptic transmission rates.

Changes in other physiological mediators of behaviour can affect neural circuitry at many different levels (e.g. brain, periphery) to produce changed behaviour during contests. This category of changes includes increases or decreases in circulating steroid hormone or catecholamine levels, modifications to brain monoamine metabolism, alterations in brain neuropeptide expression and production, and changes in the density of receptors that bind hormones.

Changes in corticosteroid and androgen titres as a result of fighting experience have historically received the most attention. Elevated levels of corticosteroids (pituitary-adrenocortical hormones that increase in titre during stress) are often discovered in individuals that have recently lost a fight (e.g. Hannes, Franck & Liemann, 1984; Huhman *et al.*, 1991, 1992; Schuett *et al.*, 1996; Sakakura, Tagawa & Tsukamoto, 1998; Schuett & Grober, 2000; Overli *et al.*, 2004). Absolute levels of corticosteroids often correlate well with the amount of aggression the loser received during the fight (Winberg & Lepage, 1998; Elofsson *et al.*, 2000; Sloman *et al.*, 2001). The effect of winning experiences on corticosteroid levels seems to vary among species; winners of some species exhibit pronounced increases in corticosteroid levels similar to that of the losers, while others do not show a significant change (e.g. Hannes *et al.*, 1984; Overli, Harris & Winberg, 1999*a*; Ramos-Fernandez *et al.*, 2000). Even within species, winner effects on corticosteroid levels may also vary between different morphs (e.g. tree lizards *Urosaurus ornatus*; Knapp & Moore, 1996). Studies of post-fight temporal changes in corticosteroid levels reveal that, although winners might experience increased stress hormone levels immediately after a fight, they return to baseline much more rapidly than losers (Hannes *et al.*, 1984; Overli *et al.*, 1999*a*; Summers *et al.*, 2003*b*).

In social groups, the relationship between dominance status and corticosteroid levels is less clear; hormone titres can correlate positively, negatively, or not at all with social rank (e.g. Overli *et al.*, 1999*b*; Sloman *et al.*, 2000; Muller & Wrangham, 2004; Sands & Creel, 2004; Weingrill *et al.*, 2004). Variation in status-related corticosteroid levels is probably not random, but rather linked to social system (e.g. Abbott *et al.*, 2003) and so-called allostatic load (e.g. Goymann & Wingfield, 2004). Although elevated levels of corticosteroids after fighting may cause the losers to retreat from further agonistic interactions, it is probably not responsible for winners persisting longer in future fights.

Experience effects on gonadal hormone levels also seem to vary among species, with the effect of winning being less detectable than the effect of losing. Depressed plasma testosterone levels usually accompany defeat in rhesus monkeys (*Macaca mulatta*), rodents, and birds (Bernstein, Gordon & Rose, 1983; Harding, 1983; Leshner, 1983; Huhman *et al.*, 1991), and, at least in fishes, may be related to subordinates producing less gonadotropin-releasing hormone in the forebrain preoptic area (Fox *et al.*, 1997). However, in copperhead snakes, no significant difference in plasma testosterone level was detected among winner, loser, and naïve individuals (Schuett *et al.*, 1996; see also Neat & Mayer, 1999). And, in fishes, some studies reported no consistent differences in plasma gonadal hormone concentrations between winners and losers (Leshner, 1983; Liley & Kroon, 1995) although others observed lower testosterone or 11-ketotestosterone levels in losers (Leshner, 1983; Cardwell & Liley, 1991; Oliveira, Almada & Canario, 1996).

A direct association between winning experience and elevated androgen levels is rarely observed (e.g. Elias, 1981; Booth *et al.*, 1989; Elofsson *et al.*, 2000) even though many studies have shown that individuals with higher (natural or exogenous) testosterone levels frequently behave more aggressively or achieve higher status than ones with lower testosterone levels (e.g. Allee *et al.*, 1955; Fernald, 1976; Silverin, 1980; Leshner, 1983; Villars, 1983; Cardwell & Liley, 1991; Higby, Beulig & Dwyer, 1991; Zielinski & Vandenbergh, 1993; Ruiz-de-la-Torre & Manteca, 1999; but see Yang & Wilczynski, 2002 for a novel interpretation). In fact, a recent study by Trainor, Bird and Marler (2004) demonstrated in California mice (*Peromyscus californicus*) that winning experience alone does not facilitate increased aggression but that winning coupled with elevated testosterone does. Moreover, winners among male orange morphs of the tree lizard (*U. ornatus*; Knapp & Moore, 1996) had lower plasma testosterone levels than naive controls 24 h after the contest. Winners of male swordtail (*X. helleri*) contests also showed depressed androgen levels 20 min after a fight, although they rose above control levels 24 h later (Hannes *et al.*, 1984). Therefore, even though losing experiences may influence testosterone levels and cause losers to behave less aggressively in some species, the association between testosterone levels and winning experiences is quite unclear in most species. It is also not clear whether elevated corticosteroid levels cause depressed testosterone levels or whether the changes merely coincide following a losing experience (Leshner, 1983). Some evidence suggests that corticosteroids inhibit androgen (e.g. testosterone, 11-keto-testosterone in fishes) production by retarding the steroidogenic activity of the gonads (Pankhurst & Van Der Kraak, 2000; Consten, Lambert & Goos, 2001, Consten *et al.*, 2001).

Serotonin (5-hydroxytryptamine; 5-HT) has been associated with aggressive behaviour (e.g. Saudou *et al.*, 1994; Cases *et al.*, 1995; see Weiger, 1997 and Edwards & Kravitz, 1997 for reviews) and dominance status (Winberg & Nilsson, 1993*a*). In vertebrates, increased serotonergic activity is generally associated with decreased aggression levels. For instance, previously dominant lizards (*Anolis carolinensis*) in which 5-HT reuptake is blocked (i.e. facilitating chronic 5-HT elevation) exhibit fewer attacks and displays and often lose to opponents that they dominated in the recent past (Larson & Summers, 2001). In invertebrates, however, increased serotonergic activity exerts the opposite effect on

aggression (Weiger, 1997). Infusion of 5-HT into the body cavity of crayfish (*Astacus astacus*) causes animals to persist longer in aggressive contests (Huber *et al.*, 1997; Huber & Delago, 1998).

The lizard and crayfish examples provided above demonstrate that 5-HT can cause changes in aggressive behaviour and/or dominance status. A question that is more relevant to this review is whether serotonergic activity is modulated by past fighting experience. Serotonin enhanced the excitability of the lateral giant neuron in dominant crayfish but inhibited it in subordinate individuals as a result of differential activation and/or differential expression of 5-HT receptor subtypes (5-HT$_1$ and 5HT$_2$; Yeh, Fricke & Edwards, 1996). Interestingly, if subordinates were isolated or allowed to become dominant, the enhancing effects of 5-HT were restored within 8–12 days; prior dominants that become subordinate, however, experienced much delayed inhibition (>38 days; Yeh, Musolf & Edwards, 1997). These results suggest that prior fighting experiences modulate neural function in crayfish and, more importantly, that 5-HT receptor expression might be related to long-term experience-dependent changes in behaviour.

In vertebrates, evidence that fighting experience modulates serotonergic activity has been demonstrated particularly well in salmonid fishes (e.g. Winberg & Nilsson, 1993*a*) and lizards (*A. carolinensis*; Summers, 2001). Subordinate arctic charr (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*) exhibit significant increases in serotonergic activity relative to dominant animals in both dyadic (Winberg & Nilsson, 1993*b*) and group settings (Winberg, Nilsson & Olsen, 1991, 1992; Hoglund, Balm & Winberg, 2000); serotonergic activity is measured as the ratio between 5-hydroxyindoleacetic acid (5-HIAA), the major serotonin metabolite, and 5-HT. Although winners experience rapid increases in 5-HT metabolism following a fight, the effect dissipates within 24 h, while the effect persists significantly longer (e.g. 7 days) in losers (Winberg & Lepage, 1998; Overli *et al.*, 1999*a*). Dominant and subordinate *Anolis carolinensis* lizards exhibit similar absolute and temporal trends for 5-HIAA/5-HT (Summers *et al.*, 1998, 2003*b*). These results are particularly interesting because status-dependent differences in the time course of serotonergic activity provide a potential mechanism underlying differences in the persistence of winner and loser effects. All of the studies mentioned above, however, examined temporal changes in serotonergic activity in dominant-subordinate pairs that cohabitated for different periods of time. A direct link to experience effects would require that serotonin metabolism be quantified over time in the absence of further social interaction.

The effects of serotonin probably are not independent of other central or peripheral mechanisms that either shape aggressive behaviour or respond to fighting experience. Induction of the 5-HT$_{1A}$ receptor increases glucocorticoid production (Fuller, 1990; Winberg *et al.*, 1997), stimulates pituitary adrenocorticotropin hormone release (Hoglund, Balm & Winberg, 2002), and mediates corticotropin-releasing hormone (CRH) – a neurohormone that modulates hypothalamic-pituitary-adrenal activity-production in the mammalian hypothalamus (Chaouloff, 1993; Dinan,

1996). Furthermore, CRH, corticosterone, and testosterone modulate brain serotonergic activity in lizards and mammals (Flügge *et al.*, 1998; Summers *et al.*, 2000, 2003*a*). These results suggest that prior experiences likely mediate future behaviour *via* a set of complex interactions among central and peripheral neuroendocrine circuits/axes.

Apart from corticosteroids, androgens, and 5-HT, many other hormone, neurohormone, and biogenic amine systems can be seen as candidates for modulating behavioural changes after winning and losing experiences. Although it is beyond the scope of this review to discuss each of these in turn, we mention a few here. Subordinates exhibit higher noradrenergic activity in some brain regions (Overli *et al.*, 1999*b*), increased plasma β-endorphin (Huhman *et al.*, 1991) and progesterone (Trainor *et al.*, 2004) levels, increased dopamine D2 receptor density (Lucas *et al.*, 2004), persistent upregulation of pro-opiomelanocortin (POMC) mRNA expression (Winberg & Lepage, 1998), and increased blood octopamine levels (in invertebrates; Sneddon *et al.*, 2000). With respect to these same neuroendocrine effects, dominant animals show either no change or opposite effects as losers. Dominant animals also exhibit marked increases in dopamine metabolism (Winberg *et al.*, 1991; Kudryavtseva, 2000). Increased γ-amino butyric acid (GABA) neurotransmission, *via* the infusion of a GABA$_A$ receptor antagonist, abolishes conditioned defeat in Syrian hamsters (*Mesocricetus auratus*) but does not inhibit the expression of submissive behaviour, suggesting a link between neurotransmitters associated with learning and the loser effect (Jasnow & Huhman, 2001). Jasnow *et al.* (1999) discovered that conditioned defeat was also probably mediated *via* the effects of the central CRH system, rather than the downstream actions of CRH (e.g. facilitation of adrenocorticotropin hormone release from the pituitary). Recent studies have implicated aromatase (enzyme that converts testosterone to estradiol; Silverin, Baillien & Balthazart, 2004; Trainor *et al.*, 2004), arginine vasotocin (e.g. Goodson, 1998), and motor circuits (Hofmann & Stevenson, 2000; Savage *et al.*, 2005) in the regulation of aggressive behaviour and experience. Importantly, at least one study has urged researchers not to overlook potential sex differences in hormone systems triggered by winning and losing experience (Davis & Marler, 2003). It is worth noting that many studies on experience effects use only males as study subjects (but see Chase, Tovey & Murch, 2003), and that when both sexes are examined, sex differences in winner and loser effects do exist (e.g. Huhman *et al.*, 2003; male Syrian hamsters exhibit a loser effect but females do not).

Changes in the neuroendocrine system after a fighting experience may have other effects on organisms. Many of these ancillary effects might be viewed as costs of maintaining high hormone levels or permanently changed receptor characteristics. Subordinate animals have been reported to decrease movement rates, modify their spatial orientation, lose body mass, increase their level of risk assessment, and experience suppression of humoral immunity (e.g. Jasnow *et al.*, 2001; Earley, Blumer & Grober, 2004). Increased testosterone and corticosteroid levels, often associated with winning and losing experiences, respectively, can decrease immune system responses (Buchanan, 2000; Casto, Nolan

& Ketterson, 2001) but it is unknown whether these hormones exert independent influences on immune suppression (Slater & Schreck, 1993; Casto *et al.*, 2001).

With these potential costs associated with other important behavioural and physiological characteristics, hormone titres might be modulated in relation to the benefit in future contests and the costs of increased hormone levels (Oliveira *et al.*, 2002). If B and C vary among individuals or even among situations for the same individual, the rate of disappearance of the effect of hormonally mediated experience effects could also vary. This disappearance could reflect either the changes in titres or changes in responsiveness to the hormone titres. In either case, we might predict that organisms would show variable rates of decay of the effect of contest experience. Such observations are common across species of fish with some showing effects that disappear within 60 min and others having effects that last more than 48 h [see Section II (4)]. The differential costs of maintaining particular hormone titres might also be responsible for the asymmetry of effects of winning and losing experiences reported for many species [Section II (3)].

During and after aggressive contests, additional physiological changes associated with energy metabolism may occur in synchrony with modifications to the neuroendocrine circuitry. In Section II (2), energy depletion and physical exhaustion were introduced as potential confounding effects in the study of winner and loser effects, particularly because the naïve opponents used to test experience effects are not subject to the physical demands of fighting before confronting prior winners or losers. Differential changes among winners and losers in post-fight energy reserves or accumulation of anaerobic metabolites (e.g. lactate), however, may be important components of experience effects. Many studies across diverse taxa have demonstrated that aggressive contests are metabolically or energetically costly for both winners and losers (but see Thorpe *et al.*, 1995; Cleveland, 1999). Fighters experience increased muscle or plasma lactate accumulation, glycolytic activity, heart rate, and oxygen consumption (e.g. Haller, 1992; Hack, 1997*b*; Grantner & Taborsky, 1998; Neat *et al.*, 1998; Sneddon, Huntingford & Taylor, 1998; Sneddon, Taylor & Huntingford, 1999; Rovero *et al.*, 2000; Schuett & Grober, 2000; Briffa & Elwood, 2001, 2002). In addition, energetic costs often increase as a function of contest duration, intensity, or the number of attacks received (e.g. Haller, Kiem & Makara, 1996; Neat *et al.*, 1998; Briffa & Elwood, 2001; but see Schuett & Grober, 2000), suggesting that prolonged fights pose further metabolic challenges.

Most relevant to this review are instances where winners and losers exhibit different metabolic responses to agonistic encounters. When differences between winners and losers do occur, losers often exhibit more pronounced increases in, for instance, plasma or muscle lactate levels (Neat *et al.*, 1998; Schuett & Grober, 2000) and glycogen metabolism (Haller, 1992). These data imply that fights are more energetically costly for eventual losers. Despite the dearth of studies on the energetic costs of fighting, if differences in the metabolic profiles or recovery times between winners and losers consistently emerge and, if accumulation of anaerobic

metabolites or reduced energy stores influence subsequent fighting behaviour (e.g. decreased propensity to initiate contests or win; but see Thorpe *et al.*, 1995), then energetic costs should be considered as an important factor mediating experience effects. Furthermore, potential interactions between glucocorticoid levels and metabolic recovery (Schuett & Grober, 2000) implicate neuroendocrine processes and metabolism as non-independent regulators of fighting behaviour following a win or loss.

IV. INTEGRATING EXPERIENCE INFORMATION

Presumably the information derived from experience could modify baseline perceptions of costs based on cues that would be used by naive individuals at the onset of contests, including opponent size and/or markings, or perceptions of costs based on one's own ability independent of the opponent. Information about perceived costs, which reflects perceived fighting ability, in a future contest might come from one or more prior experiences (e.g. Alexander, 1961; Hsu & Wolf, 1999). Prior wins or losses also can have asymmetric effects on the outcome of the present contest (see review in Chase *et al.*, 1994; Schuett, 1997; Hsu & Wolf, 1999). To understand how prior experience influences contest outcomes requires a model that can include asymmetric or symmetric effects of prior wins and losses and can integrate multiple experiences by a single individual. The model needs to be sufficiently general that it can incorporate differences in effect among past experiences and the changing value of the information over time.

Numerous learning models are relevant to a general model of integration of contest experience into a changed perception of C (Kacelnik *et al.*, 1987). Memory window models assume that prior experiences are weighted relative to the current experience (e.g. Cowie, 1977). The weighting parameter could make the most recent experience determine the perception of costs or have very little effect on the perception of costs. The latter situation usually means that a large number of prior experiences are crucial to the current perception. The weighting parameter presumably is influenced by variation in the environment. If the environment is changing then the value of experiences may also change as a function of time. Rapidly changing environments would make information from recent experiences most valuable while slow changes would tend to equalize the value of past experiences (e.g. Devenport & Devenport, 1994). Some models of learning also incorporate temporal changes in the effect of an experience, even without additional experiences (e.g. Harley, 1981). The models differ in whether the information returns through time to that of a naive individual or to some residual, modified perception of the situation in the absence of new experiences (Harley, 1981). If applied to aggression, such learning models are necessarily descriptive in the sense that experience effects would be measured by changes in contest outcome or behavioural shifts. Little information is available on the mediating physiological changes that result from experience [see Section III (2)]. But

this is not different from what psychologists often investigate in animal learning – what the organism does as a measure of learning. To make the connection between experience effects and changed contest outcomes requires an algorithm that predicts outcome from currently integrated wins or losses. This algorithm is the subject of the next section (Section V).

At least four components are necessary for a model that integrates experience effects on perceptions of C that then can be used to predict contest outcome. These include: (1) pre-experience expectations; (2) the effect of experience; (3) how that effect changes with time; and (4) how multiple experiences are integrated. We treat each of these separately before proposing a general model integrating all four components into a current expectation of costs. Organisms without experience or with no residual effects of prior experiences participate in contests. Naive individuals can still be aggressive and presumably have intrinsic estimates of the possible costs of a contest. The estimates of fighting costs should be negatively associated with fighting abilities. We indicate these intrinsic estimates of perceived fighting ability (reflected as perceptions of costs) as $\mathcal{N}_i$. Experiences then modify perceived contest costs from what would be expected by naive individuals.

A model integrating experience effects must be able to incorporate variation in initial magnitude of experience effects among contests. For example, a win might provide one magnitude of change in the perception of costs while a loss could provide a different magnitude of change (the effects obviously are of different sign). In addition, perhaps an easy win against a smaller individual might produce less change in perception of future contest costs than a difficult win against a larger individual (Beaugrand & Goulet, 2000). The asymmetry of winning and losing effects documented in many studies of experience effects on outcomes of fish contests (Table 1) could be related to these differences in initial magnitude of the effect. We use E_I to indicate the initial magnitude of effect that experience I has on changes in the perception of cost and presumably on behaviour in a subsequent contest.

The asymmetries in effects of wins and losses and how long they last could also be related to different patterns of temporal decay of the experience effects (Mackney & Hughes, 1995). The effects of single contests gradually wane, but usually winning effects disappear before losing effects (Table 1). Rate of decay can be included in the general model as a weighting function, $W_{I,t}$, that reflects changes in the effects of experience I at various times, t, after the experience. This function can be adjusted to produce any of a variety of temporal decay patterns, including no temporal decay, exponential decay, or hyperbolic decay.

An important and unstudied aspect of experience effects in contests is the pattern of decay with time or as a result of additional experiences. Some authors have included temporal decay effects in experience-based contest models, but actual 'forgetting' curves have not been documented (e.g. Bonabeau, Theraulaz & Deneubourg, 1995; see White, 2001 for possibilities). Patterns of decay will depend on the mechanism producing the experience effect (e.g. memory, hormones). Forcing decay functions to a single pattern
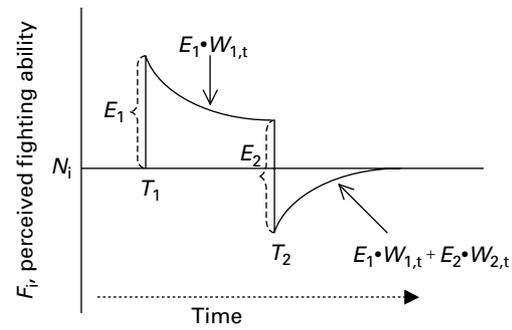

Fig. 2. Integration of experience effects for a naïve individual i with an initial perceived fighting ability (F_i) of $\mathcal{N}_i$. A winning experience at T_1 increases its perceived fighting ability by E_1. This effect decays through time and $W_{1,t}$ represents how the effect is weighted with the passage of time. A losing experience is added at T_2 and lowers individual i's perceived fighting ability by $|E_2|$ and the weighting function of this second experience is $W_{2,t}$. This combined effect gradually decays back to a perceived fighting ability of $\mathcal{N}_i$.

(e.g. a temporal weighting rule, TWR; Devenport & Devenport 1994) may miss important biological differences among organisms and situations (see Warburton, 2003 for a discussion of memory windows).

The decay of single experience effects also could be modified by additional experiences. The weighting factor, $W_{I,t}$, could signify how much the current experience modifies past effects, even with no temporal decay. This would produce a model similar to the linear operator model (Bush & Mosteller, 1951).

The full model of experience effects also must incorporate possible influences of multiple experiences and various time intervals. A simple model assumes that multiple experiences are additive, but phenomena such as blocking and interference in learning (e.g. Bouton, 1993, 1994) could make the integration of multiple experiences much more complex. Some models for the development of dominance hierarchies use multiplicative integration [section VI (4)]. At this stage virtually nothing is known about integrating multiple contest experiences, although the limited evidence is consistent with an additive model (Hsu & Wolf, 1999).

The general model that we propose is (Fig. 2):

$$F_i = \mathcal{N}_i + \sum_{I=1}^{a} (E_I \cdot W_{I,t}), \qquad (1)$$

where F_i is individual i's perceived fighting ability (in this review, reflected in perceived costs) after a fighting experiences (Bonabeau, Theraulaz & Deneubourg, 1999); $\mathcal{N}_i$ is the perceived fighting ability of individual i in the naïve state; E_I is the information individual i received and incorporated from experience I, so that for an individual that has a total of a experiences, I is any integer between 1 and a; and $W_{I,t}$ represents how the effect of experience is weighted with the passage of time or the occurrence of additional experiences. The sign of E_I is positive for a win and negative for a loss. The summation indicates that each experience is added to the remaining effects of previous experiences. If past

experience effects both decay with time and are affected by new experiences, $W_{I,t}$ becomes a complex function.

An important question is how much experience effects can accumulate for an individual or what the maximum or minimum current expectation of costs (or perceived fighting ability) can be. If the decay rate is slow enough or sequential experiences occur rapidly enough, it is theoretically possible that the total value of equation (1) could become quite large or become negative. The limits on the accumulation of experience effects become significant for several of the possible 'decision rules' that translate expectations of costs for individuals into contest outcomes [See section V]. However, one might expect a limit for the effects that reflects the type of physiological mechanisms that mediate experience effects. For example, hormone titres presumably can not increase indefinitely, but what regulates the maximum attainable values in relation to experiences is uncertain. A limit could be imposed by incorporating a scaling factor that allows F_i values to vary within a biologically meaningful range of values.

A disadvantage of the proposed model for integrating information is that it cannot explain the phenomenon of spontaneous recovery (SR), the reappearance of experience effects after a period of no experiences. Models such as the temporal weighting rule (TWR) offer an explanation for spontaneous recovery (Devenport, 1998). The critical difference between our model and SR models is that the TWR gradually approaches a long-term unweighted average of past experiences while equation (1) gradually approaches the naive condition in the absence of additional experiences. Thus, if past experiences become a 'permanent' part of the information the organism has, SR should be a significant possible outcome. The evidence for spontaneous recovery in foraging situations seems quite good (Mazur, 1996; Devenport, 1998), but the question of long-term maintenance of information has not been explored. Two bar-pressing stations that an individual has found to differ in reward rate and that are able to produce spontaneous recovery could be treated again, after a sufficiently long period of no experience (as in e.g. Mazur, 1996), as if the forager had no information about the earlier observed differences.

The question then is whether we expect individuals in aggressive situations to retain information about changed perceptions of costs for long periods. So far the evidence suggests that experience effects disappear quite rapidly and individuals revert to behaviour, or at least contest outcomes, that are consistent with having no experience. Thus, the evidence suggests that SR should not be part of the predicted outcomes of a model integrating information about contest experiences.

V. PREDICTING CONTEST OUTCOMES FROM EXPERIENCES

Modified expectations of costs resulting from prior experiences do not themselves predict contest outcomes. The outcome depends on how these expectations influence behaviour of the participants and reflects so-called decision rules (Houston, Kacelnik & McNamara, 1982) that translate experience into behaviour and how the behaviour of one contestant influences that of the other.

The perceived costs of a potential contest influence the behaviour of the opponents and the outcome of the contest. But the complexity of the combined experiences and behavioural interactions of both contestants means that individual-specific decision rules may not predict outcomes of contests. Hence, models of outcomes based on experience effects necessarily bypass several transition steps (Fig. 1) between experience and contest outcome. It may be possible, however, to develop descriptive models that incorporate experience differences into good predictions of contest outcomes.

A model that connects the effects of prior experiences to changes in contest outcome can serve as the framework for testing how mechanisms underlying experience effects influence the intermediate steps between experience and contest outcome (Fig. 1). Significant insight into the effect of experience on physiology and behaviour and how physiology and behaviour influence contest outcomes might be gained by using experience differences between contestants to predict quantitatively the outcome of contests. The effect of experience on both the intermediate stages and the final outcome of a contest should provide a good experimental tool for addressing how behaviour (physiology) of the contest participants influences the outcome of aggressive interactions. By being able to predict the final outcome, investigators may be able to focus more carefully on significant intermediate steps between experiences and outcomes (e.g. Mesterton-Gibbons *et al.*, 1996; Mesterton-Gibbons & Adams, 1998).

Trying to predict contest outcomes on the basis of experience differences leads to three general hypotheses:

(1) *Null model:* experience does not influence subsequent outcomes;

(2) *Deterministic outcome:* the individual with the higher expected B/C wins;

(3) *Probabilistic outcome:* the probability of winning depends on the difference between contestants in the effects of experience (modified B/C).

The large number of studies reviewed earlier (Table 1) that show that prior contest experience does influence the outcome leads to rejecting the null model.

The second hypothesis, developed by Hammerstein & Parker (1982), predicts that the evolutionarily stable strategy (ESS) for continuous strategy (war of attrition), asymmetric contests is for the individual that reaches the point where $B=C$ to be first to submit. This model assumes that an individual knows its own costs and benefits; some of the former may depend on the fighting ability of its opponent. Another possibility is that the contestants assess their B and C relative to their opponents' during a contest. Whether an individual assesses only its own ability or its abilities relative to those of its opponent does not influence the expected contest outcomes, but does affect predicted details of the actual contest (Mesterton-Gibbons *et al.*, 1996; Mesterton-Gibbons & Adams, 1998). These models in their simplest form predict that the individual with the higher B/C always
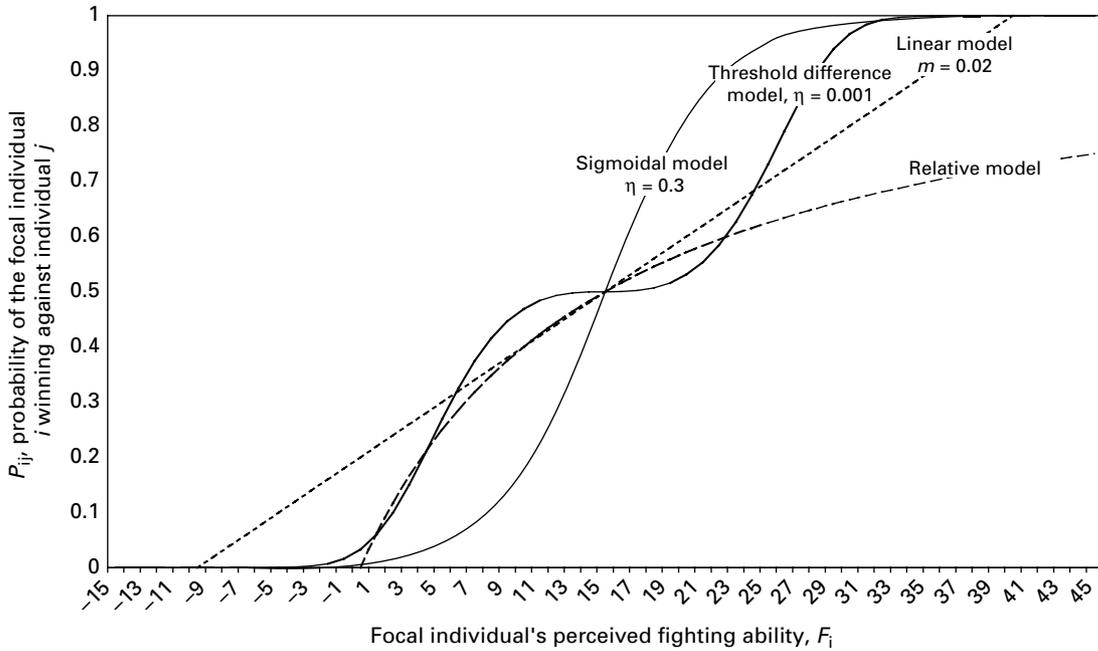
Fig. 3. Probability of winning (P_{ij}) predicted from the Linear [Section V (1), equation (2) with m arbitrarily set to 0.02], the Relative [Section V (1), equation (3)], the Sigmoidal [Section V (1), equation (4) with η arbitrarily set to 0.3], and the Threshold difference models [Section V (1), equation (5) with η arbitrarily set to 0.001] for a focal individual i with various perceived fighting ability (F_i) fighting against an opponent j with a perceived fighting ability (F_j) of 15.

wins, no matter the difference in B/C is between the contestants.

Mistakes in the assessment of one's own B/C or that of the opponent may lead to the individual with the lower B/C winning, particularly when the B/C values of the contestants are similar. Even if hypothesis (2) is correct as a model for determining the winner of a contest, the probability of mistakes in assessment by the participants means that the outcome will be probabilistic. The probability of winning should approach 0.5 as the B/C of the opponents become more similar and should approach 1 or 0 as the differences become more extreme. We can hypothesize that as the difference in experience effects increases for two contestants the probability of winning for the contestant with the greater winning experience also increases above what it would be for naive individuals. This means that the relation between the changed probability of winning and the difference in experience effects is a monotonically increasing function (all four lines in Fig. 3).

(1) Models based on experience differences between contestants

The biological explanations of these patterns are potentially quite complex, but can be summarised with some fairly general comments. We consider only the changed outcome as mediated by a series of experiences for each contestant. Significant contributions from experience differences result in outcomes that are modified considerably from what is expected for naive individuals. Various combinations of influences of experience and intrinsic characteristics can produce different relationships between changed contest

outcome and experience differences among the individuals. We propose four models that integrate the intrinsic fighting abilities and prior fighting experiences of two opponents into their fighting outcome (Fig. 3). Each of these models provides a means of linking experience with contest outcome *via* a decision rule. However, they differ in (1) whether or not fighting outcome is determined by the absolute or relative difference in perceived fighting abilities between two opponents, and, (2) if fighting outcome is determined by the absolute difference, whether or not the importance of the experience effect is dependent on the magnitude of the difference.

Model 1 is a **Linear** model and can be written as:

$$P_{ij} = 0.5 + m(F_i - F_j) = 0.5 + m\left[\left(N_i + \sum_{I=1}^{a}(E_I \cdot W_{I,\iota})\right) - \left(N_j + \sum_{J=1}^{b}(E_J \cdot W_{J,\iota})\right)\right] \quad (2)$$

$$(0 \leqslant P_{ij} \leqslant 1),$$

where P_{ij} is the probability of individual i winning against individual j; F_i is individual i's perceived fighting ability after experiences [see Equation (1) in Section IV]; F_j is individual j's perceived fighting ability after experiences. The slope, m, scales how important differences in the experience-modified perceived fighting ability are to contest outcome. In this model, the probability of winning is a linear function of the absolute difference in the perceived fighting abilities. The importance of the experience effect on the probability of winning ($= m$) is independent of the fighting ability of the two opponents.

Model 2, the **Relative** model, can be written as:

$$P_{ij} = \frac{F_i}{F_i + F_j}$$

$$= \frac{\mathcal{N}_i + \sum_{I=1}^{a}(E_I \cdot W_{I,t})}{\left[\mathcal{N}_i + \sum_{I=1}^{a}(E_I \cdot W_{I,t})\right] + \left[\mathcal{N}_j + \sum_{\mathcal{J}=1}^{b}(E_{\mathcal{J}} \cdot W_{\mathcal{J},t})\right]}$$

$$(0 \leqslant P_{ij} \leqslant 1). \quad (3)$$

In this model, the probability of winning is determined by the relative perceived fighting ability of the two opponents. Consequently, the influence of the experience effect is negatively scaled by the sum of the perceived fighting ability of the two opponents. Experience effects are more difficult to detect among bigger contestants or contestants with more winning experiences. Perhaps, as in Weber's law in psychology, as contest intensity increases it requires a greater difference between individuals to produce the same outcome change.

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

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

$$= \frac{1}{1 + e^{-\eta\left\{\left[\mathcal{N}_i + \sum_{I=1}^{a}(E_I \cdot W_{I,t})\right] - \left[\mathcal{N}_j + \sum_{\mathcal{J}=1}^{b}(E_{\mathcal{J}} \cdot W_{\mathcal{J},t})\right]\right\}}}, \quad (4)$$

where η scales the rate of approach to the asymptote. A large η produces a more deterministic outcome that means a small difference in the experience-modified perceived fighting ability would be almost sufficient to ensure the winning of the opponent with a slightly higher perceived fighting ability. Any further increases in the difference will have very little effect on the fighting outcome. On the other hand, with a small η, differences in experience-modified perceived fighting ability have a more gradual influence on fighting outcomes. Nonetheless, the change in effect diminishes as the difference increases.

Model 4, the **Threshold difference** model, can be written as:

$$P_{ij} = \frac{1}{1 + e^{-\eta(F_i - F_j)^3}}$$

$$= \frac{1}{1 + e^{-\eta\left\{\left[\mathcal{N}_i + \sum_{I=1}^{a}(E_I \cdot W_{I,t})\right] - \left[\mathcal{N}_j + \sum_{\mathcal{J}=1}^{b}(E_{\mathcal{J}} \cdot W_{\mathcal{J},t})\right]\right\}^3}}. \quad (5)$$

In this model, small differences in the perceived fighting abilities do not produce detectable effects on fighting outcomes. But once the differences become sufficiently large (i.e. beyond a threshold) then changes occur rapidly toward the asymptote. The parameter η controls both (1) the width of the interval where fighting outcome remains insensitive to the difference in perceived fighting ability, and (2) how fast the probability of winning approaches the asymptote once the difference reaches the threshold. For instance, with a smaller η, a bigger difference in perceived fighting ability is needed to produce a recognisable effect on the fighting outcome and the probability of winning approaches the asymptote at a slower rate.

The Linear and the Relative models theoretically could yield $P_{ij} < 0$ or > 1.0 if experience effects can accumulate to extreme differences. It is obvious that $P_{ij} < 0$ or > 1.0 are empirical impossibilities. However, the theoretical possibility means that even with temporal decay of experience effects, the probability of winning (losing) could remain at 1 or 0 for some period of time until the combined experience effects decay to values that yield wining probabilities between 0 and 1. P_{ij} in the Sigmoidal and the Threshold difference models is bound between 0 and 1.

The models, as noted earlier [section II (3)], make different predictions about symmetry of outcome effects from winning and losing experiences, even if the initial effect of an experience (E_I) and the weighting function are equivalent for wins and losses. The Linear, the Sigmoidal and the Threshold difference models predict that, once integrated, wins and losses have the same effect on the probability of winning while the Relative model predicts an asymmetric effect of winning and losing experiences on contest outcomes. This predicted outcome asymmetry based on symmetric experience effects could explain why losses have more effect than wins in many contests and may explain why the influence of winning or losing may disappear/decay at varying time intervals/rates (e.g. Francis, 1983; Bakker *et al.*, 1989; Chase *et al.*, 1994).

(2) Models based on escalation probabilities

The interaction between experience and contest outcome is mediated by changes in behaviour of the contestants. A contest is a sequential series of interactions between the individuals, with each individual having the option of terminating or continuing the contest at any time. For contests that terminate early, before escalation makes reliable information about actual fighting ability available, prior experience might play a major role in the contest outcome [Section II (1)]. These considerations suggest a more complex relationship between experience effects and outcomes than represented by equations (2)–(5). This leads to a differently detailed model predicting contest outcomes that partitions sequential interactions in a contest into early stages that are subject to experience effects and later stages that are not influenced by prior experiences but depend only on intrinsic fighting ability:

$$P_{ij} = a_{ij}(1 - e_{ij}) + b_{ij}(e_{ij}), \quad (6)$$

where P_{ij} equals the probability of individual i winning against j, a_{ij} is the probability of i winning nonescalated contests against j, b_{ij} is the probability of i winning escalated contests against j, and e_{ij} is the probability that a contest will escalate. An escalation occurs only when both opponents are willing to participate; therefore, $e_{ij} = e_{ji}$. The three variables on the right-hand side of equation (6) should be related predictably to how experience changes the behaviour of individuals. We predict that b_{ij} should depend on intrinsic fighting ability and should be independent of experience (e.g. equal to 0.5 for size-matched fish). The other two variables either should be positive functions of increasing winning experience (e_{ij}), or an increasing difference in winning experience (a_{ij}).

As discussed in Section II (1), preliminary data from mangrove rivulus contests support this general relationship (Hsu & Wolf, 2001). The outcome of escalated contests (those involving mutual attacks and physical interactions) is not statistically different from 50:50 for size-matched individuals with different experience backgrounds and is biased toward individuals with more winning experience in non-escalated contests (those resolved with displays or with an attack by only one individual and retreat by the opponent). Similar results were obtained in green swordtail fish *X. helleri* where previous winners were significantly more likely to win non-escalated than escalated contests (Earley & Dugatkin, 2002).

An important question related to equation (6) is how experience changes the sequential behaviour of individuals to change a_{ij} and e_{ij}. As an example, consider the relation between experience, initiation strategy, and contest outcome. Data from mangrove rivulus contests indicate an initiator that attacks wins approximately 90 % of contests (30 of 32); an initiator that displays wins 52 % of the time (50 of 96) (Hsu & Wolf, 2001). The question is how experience influences whether the initiator displays or attacks. The relationship between a_{ij} or e_{ij} and experience leads to four general alternative hypotheses:

H_1: the difference in experience of the two individuals (relative or absolute) is correlated with each variable (a_{ij}, e_{ij});
H_2: only the experience of the individual with more winning experience is correlated with each variable;
H_3: only the experience of the individual with more losing experience is correlated with each variable;
H_4: the sum in experience of the two individuals is correlated with each variable.

To make quantitative predictions to test these hypotheses requires measuring how much experience has changed expectations of costs. Data from Hsu & Wolf (2001) suggest that H_1 is supported for a_{ij} while for e_{ij}, H_1 is rejected; and not enough data are available to distinguish among H_2, H_3, and H_4. The difference between experience effects is positively related to the probability of winning non-escalated contests (a_{ij}) by the opponent with the higher experience effects ($r^2 = 0.96$; $N = 5$; $P = 0.0004$). On the other hand, this difference does not predict the probability that the contest will escalate (e_{ij}), which is probably better predicted by level of cost expectation of each contestant or the summed cost expectations of both. These limited data suggest that the outcome of fights thus depends on how experience modifies the tendency of contestants to escalate contests. The greater the winning experience the more likely the contest is to escalate, in which case experience will no longer influence the outcome. On the contrary, with greater loser effects, fewer contests will escalate and the outcome of non-escalated contests will be more predictable from prior experience.

VI. EXPERIENCE EFFECTS ON DOMINANCE HIERARCHIES

Many animals live in social groups or form transient aggregations at certain times of the year (e.g. the reproductive season). Linear dominance hierarchies are common in such groups and status within these hierarchies may have important fitness consequences in the form of feeding or reproductive opportunity (Ellis, 1995). If individual A dominates B, B dominates C, and A also dominates C in all component triads of a group then relationships are transitive and the hierarchy is linear. Introducing intransitive circularities reduces linearity. Considerable debate remains regarding the mechanism(s) that promote linear hierarchy formation. Can success in rank-order fights be attributed solely to individual characteristics that correlate well with dominance? Is hierarchy formation governed by winner and loser effects? Do both individual attributes and experiences shape the developing hierarchy? In this section, we discuss the influence of individual intrinsic attributes (e.g. size, weaponry, aggression levels) and contest experience on hierarchy structure with emphasis on the properties of the winner and loser effects discussed in Section II.

(1) Basic models and empirical evidence

Early work on social organisation in animals assumed that a hierarchy was simply an amalgam of dyadic relationships, the outcomes of which were based only on factors intrinsic to the individuals (e.g. size, age, physical prowess; Schjelderup-Ebbe, 1922, 1935; Ginsburg & Allee, 1942; Collias, 1943; Allee *et al.*, 1955). This led to two basic models of linear hierarchy formation – the correlational and tournament models (see Chase, 1974, for a review). The correlational model posited that a single trait or suite of traits that correspond with dyadic fighting success could predict the eventual status of an individual in a hierarchy. The tournament model asserted that the hierarchy deduced from pairwise, round-robin competitions should emerge when all tournament participants are placed together in a group. The primary difference between the two models is that the tournament model provides a potential mechanism for hierarchy establishment – outcomes of dyadic contests – while the correlational model postulates only that a statistical correlation exists between certain traits and dominance rank (Chase, 1974). The two models are similar if dyadic outcomes are based on differences in intrinsic traits related to fighting ability.

Some authors have argued that neither the correlational nor tournament model adequately predicts linear hierarchy formation in the absence of experience effects (e.g. Chase, 1974) while others have deemed individual variation in intrinsic fighting ability as paramount in determining hierarchy structure (Jackson & Winnegrad, 1988). Several recent models have demonstrated that a linear hierarchy can develop when pre-existing asymmetries in fighting ability (e.g. body size) are the sole determinant of contest outcome (Beaugrand, 1997; Bonabeau *et al.*, 1999; Beacham, 2003; also see Mesterton-Gibbons & Dugatkin, 1995, for the effects of assessment of fighting ability during rank-order contests). Models based solely on intrinsic attributes, however, neglect the influence of dynamic processes in hierarchy formation. As discussed earlier, fighting experience influences contest outcome at the dyadic level hence, it is reasonable to assume that such effects could operate during

hierarchy establishment (Barnard & Burk, 1979; Chase, 1980, 1982 *a, b*, 1985; Bonabeau, Theraulaz & Deneubourg, 1996; Dugatkin, 1997; Hemelrijk, 2000).

In his 'jigsaw model', Chase (1980, 1982 *a, b*) described linear hierarchies as an emergent property of winner effects (i.e. *double dominance*) and loser effects (i.e. *double subordination*) operating at the group level. Despite the wealth of theoretical investigations of experience effects and hierarchy formation (see below), there is little empirical evidence for the importance of winner and loser effects in the formation of linear hierarchies.

Ratner (1961) initiated an experimental method for examining the effects of prior experience on individual hierarchy status in domestic fowl that entailed removing individuals from an established group, subjecting them to defeat, and reintroducing them into the original group. In his study and later studies on cichlid fish (Nelissen & Andries, 1988) and insects (Alexander, 1961; Moore *et al.*, 1988), the general trend was for previous wins/losses to precipitate subsequent increases/decreases in rank for the experienced individual. By contrast, experiments on red jungle fowl (*Gallus gallus spadiceus*) demonstrated that flock-experienced hens always dominated flock-naïve hens regardless of the type of experience obtained in previous groupings (Kim & Zuk, 2000). In some animals either type of social experience (win or loss) may increase future contest success, possibly through training (see also Moore *et al.*, 1988; Stamps & Krishnan, 1998).

A second experimental technique for examining experiential effects on hierarchy formation is group fusion, which entails merging two established hierarchies into one larger assemblage (e.g. Yasukawa & Bick, 1983; Cristol, Nolan & Ketterson, 1990; Wiley, 1990; Cristol, 1995; Dugatkin & Earley, 2003). By controlling for individual differences in attributes related to dominance within and between groups, the influence of prior rank-order experience on post-fusion status can be examined. Although the aforementioned studies have yielded support for experience effects influencing hierarchy formation, none analysed initial hierarchy establishment to ascertain how early patterns of wins/losses in a newly formed group affected an individual's future status. Empirical tests of Chase's (1980) 'jigsaw model' suggest that *double dominance* and *double subordination* sequences are common during the formation of linear hierarchies in primates (Mendoza & Barchas, 1983; Barchas & Mendoza, 1984), birds (Chase 1985, Chase & Rohwer, 1987), fish (Chase *et al.*, 2002) and invertebrates (Goessmann, Hemelrijk & Huber, 2000). These studies were concerned primarily with how interaction sequences translate into linear hierarchies rather than tracking individual experiences and eventual status acquisition. Goessmann *et al.* (2000) examined the effects of experience on final status, in this case in groups of crayfish that had no fighting experience prior to establishing the groups. Their observations of crayfish groups showed that experiences obtained during the initial stages of hierarchy formation accurately predicted an individual's final status within the same group. These results should be interpreted with caution as the authors used a self-selection procedure, which could confound the rank-order effects of experience with the effects of initial variation in intrinsic

fighting ability among the crayfish [see Section II (2)]. Dugatkin & Druen (2004), however, employed a random selection procedure in which size-matched green swordtail males were given winning, losing, or no experience and then placed together to form a dominance hierarchy. Hierarchies in which previous winners achieved the dominant rank, naïve animals the middle rank, and prior losers the subordinate rank were significantly overrepresented. These results provide compelling evidence that winner and loser effects can affect the ordering of individuals in a social hierarchy.

Some of the most salient aspects of experience effects (e.g. symmetry) remain untested in a group context (but see Chase *et al.*, 2003). Theoretical models provide the framework for investigating how hierarchy structure changes as properties associated with experience effects are manipulated. Properties that may alter hierarchy structure or how quickly a clear rank-order emerges were discussed earlier [Section II] and are those associated with translating experience effects into contest outcomes. These include the decision rules employed, the symmetry, magnitude, and longevity of experience effects, how the effects accumulate, and the limits to changes in perceived fighting ability. While relatively little is known about these properties in contest behaviour, we discuss the theoretical influence of each on the emergent structure of a hierarchy. Table 3 provides a general overview of the similarities and differences in the parameters employed and the predictions generated by existing models of hierarchy formation. In the following sections, the terms 'dominance value' and 'dominance score' are synonymous with the perceived fighting ability of the animal in question. Although the many models that we discuss may differ in how they define 'dominance scores', our interpretation provides a level of consistency throughout this review.

(2) Decision rules

The decision rules used to determine contest outcome might be deterministic or probabilistic. When outcomes are deterministic, individuals with larger dominance values always win (Jager & Segel, 1992). When outcomes are probabilistic, individuals with smaller dominance values have a chance of winning but the probability of doing so decreases as asymmetries in dominance scores increase (Hogeweg & Hesper, 1983; Dugatkin, 1997; Hemelrijk, 2000). The likelihood that a linear hierarchy forms increases as outcomes become more deterministic (Jager & Segel, 1992; Bonabeau *et al.*, 1995). Several models that use probabilistic outcomes, however, still yield unambiguous rank orders (e.g. Dugatkin, 1997; Hemelrijk, 2000).

Three types of probabilistic decision rules have been used in theoretical models of hierarchy formation – linear, relative, and sigmoidal (see Section V and Table 3). If 'relative' decision rules are used the influence of winner and loser effects on an individual's probability of winning against an inexperienced conspecific may be asymmetrical, even when winner and loser effects have equal but opposite impacts on future dominance values [see Section II (3)]. Asymmetries in winning probabilities may be amplified further in hierarchies where winners and losers interact with individuals

Table 3. A sample of models that have assessed the influence of experience effects on hierarchy formation. S=symmetrical, A=asymmetrical, LIN=linear decision rule; REL=relative rule; SIG = sigmoidal decision rule, DET=deterministic decision rule, MULT= multiplicative, ADD=additive, ADDPF=additive with damped positive feedback; LO=lower bound, UP=upper bound, W=winner, L=loser, NA=not applicable, #=number of. Tables or figures noted below refer to those in the cited paper. When multiple papers are cited for the same author(s), the properties provided by each model are denoted by last two digits of the year.

Citation	Decision rules	Interaction probability	Accumulation of effects	Symmetry	Magnitude	Bounds of dominance values	Temporal decay	Individual recognition	Spatial distribution	Group size (N)
Landau (1951)[1]	LIN	Random	MULT	S	Constant	LO=0, UP=total #group members	No	Yes (?); bias against reversal	No	NA
Hogeweg & Hesper (1983, 1985)[2]	REL	Random (confined to the centre of the nest-space)	ADDPF	S	Constant	None	No	No	Yes	Varies with time step in simulation
Theraulaz et al. (1991)[3]	SIG; term η influences degree of determinism	Random	ADD	S	Constant	LO=0, UP=1000	No	No	Yes	6 or 13
Jager & Segel (1992)[4]	LIN or DET	Specified function	ADD	S	Variable	LO=0, UP=1	No	No	No	NA
Bonabeau et al. (1995, 1996, 1999)[5]	SIG; term η influences determinism (95, 96, 99). DET for individual attributes model (99)	Random (95), variations of four interaction patterns (Cases 1–4; 96, 99), or proportional to time spent walking on nest (99, individual attributes)	ADD	S (95, 99) or S and A (96)	Constant (95, 99) or variable (96)	Forces: LO=0, UP=# interactions per simulation; dominance index: LO=0, UP=1 (Fig. 10 in 99)	Yes (95, 96) or No (99)	No (95, 99) or Yes (96)	No	10 (95), 3 (96, 99)
Theraulaz et al. (1995)[6]	SIG; term η influences degree of determinism	Four possible interaction patterns (Cases 1–4; see Fig. 3)	ADD	S	Constant	Forces: LO=0, UP=# interactions per simulation; Dominance index: LO=0, UP=1	No	Yes	No	13
Hemelrijk (1996, 1998, 1999, 2000, 2002)[7]	REL	Random (96) or partitioned into three patterns (obligate attack, ambiguity reducing or risk-sensitive; 98, 99, 00)	ADDPF	S	Constant (96) or variable (98, 99, 00)	LO=0.01, UP=max # interactions	No	No or Yes (estimators -96, 00)	Yes	5, 8, 10 (Table 1 in 99)
Beaugrand (1997)[8]	DET	Random at first; interactions cease if dominance criteria met	ADD (Table 2)	S and A	Variable	None	No	Yes(?); see interaction probability	No	Vary from 3 to 10 or fixed at 6

Dugatkin (1997, 2001)[9]	REL	Random but can depend on ϕ = aggression threshold	MULT (W/L & bystander effects)	S and A	Variable	LO = 0	No	No	No	4, 6, 8, 12
Mesterton-Gibbons (1999)[10]	LIN	Random	ADD	NA	NA	LO = 0, UP = 1	No	No	No	NA
Albers & DeVries (2001)[11]	SIG	Distinct sequential order; all dyads interact ~ equal # times	ADDPF	S	Variable	None	No	No	No	13
Beacham (2003)[12]	DET if W or naïve animal meets loser; 50% probability of W if like meets like (threshold) LIN or curvi-linear (score differential)	Random	ADD	S (threshold)	Variable	Dynamic: depends on number of W and L with passage of time	Yes	Yes	Indirectly	6–10

[1] Larger society, stronger W/L effects needed to preserve dominance structure.

[2] W/L effects yield differentiation in dominance values and castes (common *versus* elite workers); spatial differentiation (centrality of dominants).

[3] Stable linear hierarchy emerges; individuals can be grouped into three distinct categories based on dominance values and foraging threshold (categories differ in space occupancy, interaction frequency, and interaction with dominant). Manipulating magnitude of W/L effects has little influence on structure.

[4] Probabilistic outcomes yield undifferentiated structure (all individuals converge around one dominance value); Deterministic outcomes yield differentiated hierarchy characterised by having distinct high- and low-ranking individuals.

[5] Symmetrical W/L-effects yield linear hierarchy. Deviations from symmetry hinder linearity, e.g. if W>L, despotic hierarchy; if L>W, reverse despotic hierarchy (96). No hierarchical differentiation at low density; developed hierarchy at high density – influenced by temporal decay. Hierarchy characteristics rely on decision rule with hierarchical differentiation more probable as outcomes become more deterministic (95, 96). Same hierarchy profiles obtained in self-organisation and individual attributes models (99).

[6] Probability of interaction influences hierarchy structure. Using 'forces', obtain linear hierarchy (Case 1), near-despotic (Case 2), or hierarchy with plateaus at middle ranks (Cases 3, 4). Using 'dominance index', obtain linear hierarchy (Cases 1, 3, 4) or less pronounced despotic (Case 2). Individual recognition hinders linearity (*i.e.* increases probability of intransitivity).

[7] W/L effects yield well-differentiated hierarchy (Fig. 4 in 96). As magnitude of W/L effects increase, hierarchies exhibit more pronounced differentiation, greater unidirectionality of aggression, decline in aggression with time, more stability, and spatial centrality of dominants (see 02 for synopsis). Stronger hierarchy differentiation and patterns of rank-dependent behaviour in absence of individual recognition (e.g. estimators *versus* perceivers); long-term intransitive relationships may exist among estimators.

[8] W/L effects alone or in combination yield perfectly linear hierarchies. When dominance values vary at start (without W/L effects), obtain linear hierarchies. Hierarchy differentiates faster with stronger W/L effects and larger initial asymmetries in dominance values. W/L effects play larger role when there is less initial variation in dominance values.

[9] W-effect alone yields linear hierarchy; L-effect alone yields despotic hierarchy. With L-effect constant, increasing W-effect promotes linearity; with W-effect constant, increasing L-effect hinders linearity (97). When bystander effects act in combination with W/L effects, obtain linear hierarchies; bystander effects alone yield either reverse despotic hierarchy or no hierarchy (01).

[10] Probability of linear hierarchy formation increases as magnitude of combined experience effects increases. W-effects cannot evolve independently of L-effects but L-effects can evolve independently. Winner effects strongest when there is maximum variance in actual dominance values; loser effect strongest when intermediate dominance value variance exists.

[11] As magnitude of W/L effects increases, get stronger, faster differentiation of hierarchy (rank differences become larger).

[12] Threshold model: in absence of experience effects, as variation in size distribution increases, so too does probability of linearity; experience effects alone (when magnitude <0.5 and only most recent experience affects experience score) yield majority of significantly linear hierarchies; presence of experience effects increases linearity of hierarchies, even with small variance in size distribution. Score differential model: decision rules (concave, linear, convex) affect how prior experience influences hierarchy linearity; sequential development of relationships facilitates linearity.

possessing a wide range of dominance values (scores). With the relative rule, the probability that an individual will defeat an opponent whose dominance score is x units above or below its own depends on the dominance score of the individual in question. As the difference in dominance scores between two individuals becomes larger, so too does the asymmetry in winning probabilities between animals with high and low dominance scores. By contrast, with the linear and sigmoidal rules, the probability that an individual will defeat an opponent whose dominance score is x units above or below its own is the same, regardless of the dominance score of the individual in question. The different winning probabilities generated by each decision rule may influence overt interaction frequencies and the distribution of wins and losses among individuals. Thus, the particular decision rule chosen is important in determining hierarchy dynamics and ultimately, final hierarchy structure (Beacham, 2003). Systematic examinations of how different decision rules alter hierarchy structure under similar theoretical conditions have not been conducted.

(3) Symmetry and magnitude

The presence of symmetrical (equal magnitude, opposite sign) winner and loser effects is sufficient to generate a linear hierarchy among a set of initially identical individuals (Hogeweg & Hesper, 1983; Bonabeau et al., 1995, 1999; Hemelrijk, 1996, 2000; Beacham, 2003; but see Dugatkin, 1997, where only the top rank is clear). Increases in the magnitude of experience effects often lead to more pronounced social (and sometimes spatial) differentiation (Skvoretz, Faust & Fararo, 1996; Hemelrijk, 1998, 1999, 2000; Mesterton-Gibbons, 1999; Albers & DeVries, 2001; Beacham, 2003; but see Theraulaz et al., 1991 and Dugatkin, 1997, for no effect).

This assumption of symmetry of effects may not apply in all animals [Section II (3); Bakker et al., 1989; Schuett, 1997; Goessmann et al., 2000; but see Hsu & Wolf, 1999], making it important to understand whether predicted hierarchy structures change when experience effects are asymmetrical (different magnitude, opposite sign). Beaugrand (1997) showed that linear hierarchies arise regardless of which combinations of experience effects are employed (e.g. drastic asymmetries where either winner or loser effects are absent or when both effects operate simultaneously and symmetrically in magnitude). However, different combinations of asymmetric winner and loser effects were not systematically examined. Rather, during each simulation the effects of winning and losing were drawn randomly from a normal distribution and could vary both between individuals and for each individual across contests. Both Bonabeau et al. (1996) and Dugatkin (1997) methodically pitted winner and loser effects against one another in attempts to tease apart both the independent effects of victory and defeat and the consequences of asymmetries on hierarchy structure. Bonabeau et al. (1996) revealed that deviations from symmetry in either direction hinder linearity. Dugatkin (1997) demonstrated increased linearity as winner effects became more influential but showed that stronger loser effects lead to despotic hierarchies where only the top

rank is clear. The fact that substantial species-specific differences exist in the symmetry and magnitude of experience effects should provide the impetus to test these conflicting predictions.

Still other models adjust the magnitude of experience effects using a 'damped positive feedback' mechanism whereby winner and loser effects become more pronounced when the outcome of a contest is unexpected, e.g. when individuals with lower dominance scores win (Hogeweg & Hesper, 1983; Jager & Segel, 1992; Hemelrijk, 1996, 1998, 2000; Albers & DeVries, 2001). A recent study on swordtail fish provides equivocal support for this 'damped feedback' mechanism. Individuals that won/lost contests against matched opponents exhibited greater experience effects than those that won/lost against much smaller/larger opponents (Beaugrand & Goulet, 2000). Because a self-selection procedure was required to conduct this study, however, it is unclear how much of the difference in experience effect could be attributed to individual attributes versus winning or losing against different types of opponents.

(4) Accumulation of effects

One of the most apparent differences among the models detailed in Table 3 is how the effects of winning and losing accumulate for an individual. Some models employ additive experience effects (Hogeweg & Hesper, 1983; Bonabeau et al., 1995, 1996, 1999; Theraulaz, Bonabeau & Deneubourg, 1995; Hemelrijk, 1996, 1998, 1999, 2000; Beaugrand, 1997; Beacham, 2003) while others use multiplicative effects (Landau, 1951; Dugatkin, 1997). Section IV of this review describes a general model in which experience effects accumulate additively [Equation 1]. Conversely, if F_i is successively multiplied by the magnitudes of each winner and loser effect (E_a) weighted for the passage of time ($W_{a,t}$), then experience effects accumulate multiplicatively and:

$$F_i = \mathcal{N}_i \cdot \prod_{a=1}^{n_{win}} (1 + E_{win} \cdot W_{a,t}) * \prod_{b=1}^{n_{lose}} (1 - E_{lose} \cdot W_{b,t}) \quad (7)$$

where n_{win} and n_{lose} represent the total number of winning and losing experiences, respectively, $W_{a,t}$ and $W_{b,t}$ provide different weights for different winning and losing experiences, respectively, $\mathcal{N}_i$ is the intrinsic estimate of fighting ability in an inexperienced animal, E_{win} is the magnitude of the winner effect, and E_{lose} is the magnitude of the loser effect.

When winning and losing influence additively an individual's future dominance ability, hierarchy differentiation may occur at a slower rate than when the effects are multiplicative. This alone should not alter the final structure of the hierarchy (e.g. which rank each animal attains). The properties imposed on the hierarchy under additive or multiplicative conditions, however, are arguably quite different (e.g. differences in perceived fighting abilities between adjacent-ranking animals). When effects are additive, winning and losing change dominance scores in the same way irrespective of current dominance ability (e.g. x dominance units are added to or subtracted from a fighter's overall

score). When multiplicative, the magnitude of the experience effects depends on an individual's own dominance value. Here, both winning and losing have far greater effects on individuals with high dominance scores than on individuals with low dominance scores. Whether experience effects alter dominance values in a manner that depends on current dominance ability has yet to be empirically tested. Regardless of the symmetry between winner and loser effects and with the assumption that all group members begin with equal fighting abilities, additive effects yield qualitatively linear hierarchies in which individual ranks are evenly spaced. For example, if the difference between α and β individuals is five perceived fighting ability units, then the difference between β and γ or γ and ω individuals is also five units. By contrast, multiplicative effects induce drastic asymmetries in perceived fighting ability among top-ranking individuals but negligible asymmetries at lower ranks if sufficient interactions occur. The hierarchies are still qualitatively linear, but quantitatively they appear more despotic in form, with only the top ranks clearly defined. Examining rank-related and temporal patterns of aggression may help to shed light on how experience effects accumulate and subsequently influence social structure (Freeman, Freeman & Romney, 1992; Oliveira & Almada, 1996; Castro & Caballero, 1998; Savino & Kostich, 2000; Forkman & Haskell, 2004). Additive and multiplicative models clearly impose drastic structural differences on the hierarchy that may be important when considering rank maintenance, stability, and even the socio-spatial properties of the group (e.g. if rank-distance also reflects physical distance; Hemelrijk, 2000). It is also important to note that, regardless of how winner and loser effects accumulate the sequence in which they are experienced might influence differences in dominance scores between any two individuals in a hierarchy, and thus interpretations of the rank order (see 'final score' *versus* 'cumulative score' in Hopkins, 1987).

(5) Bounds of experience effects

In both additive and multiplicative models, winner effects can theoretically increase perceived dominance abilities without bound. Additive models possess no theoretical lower bound but, in multiplicative models, individual abilities cannot decrease past zero. In most models, the convention is to set a lower bound (usually at or approaching zero) and to have an upper bound that depends on the total number of interactions (Bonabeau *et al.*, 1995, 1996; Theraulaz *et al.*, 1995; Hemelrijk, 1996, 1998, 1999, 2000; Dugatkin, 1997; but see Theraulaz *et al.*, 1991 where upper bound for 'force' was set at 1000 units). This is akin to acknowledging that individual dominance ability cannot plummet to unreasonably low levels but that it may, in fact, grow quite large.

Both the upper and lower limits of dominance ability are likely to be constrained by physiological, temporal, or behavioural factors (e.g. Bonabeau *et al.*, 1999; Section V). Bekoff & Dugatkin (2000) found that an individual's probability of winning future encounters plateaus after three successive wins in coyotes (*Canis latrans*). In addition, effects of hormones known to be involved in stress or agonistic

responsiveness (e.g. glucocorticoids and androgens) are unlikely to be infinitely large because of limits on receptor density or the initiation of negative feedback cascades. Furthermore, if experience effects decay temporally, the opportunity to reach infinitely large or small dominance scores is reduced.

The extent to which perceived dominance abilities are bounded may shed some light on why predictions of hierarchy structure differ among theoretical models. When dominance scores are unbounded in either direction, winner effects alone and loser effects alone each promote linearity; otherwise, they do not appear capable of doing so (see comparisons of Bonabeau *et al.*, 1996; Beaugrand, 1997; and Dugatkin, 1997 in Table 3). If wins or losses are distributed unevenly among group members and if individuals are capable of assessing their own dominance ability as well as that of others, a linear hierarchy should form under unbounded conditions (Dugatkin, 1997, for winner effect; Beaugrand, 1997, for both effects). Hierarchy structure changes when upper and lower bounds are implemented. When dominance scores have an upper limit, winner effects alone yield 'reverse despotic' hierarchies where only the most subordinate rank is clear (Bonabeau *et al.*, 1996). Similarly, when dominance scores have a lower limit (0), loser effects alone yield despotic hierarchies where only the top rank is clear (Bonabeau *et al.*, 1996).

When both winner and loser effects operate simultaneously, linear hierarchies often form regardless of whether bounds are employed (e.g. Bonabeau *et al.*, 1996 *versus* Beaugrand, 1997 in Table 3). This suggests that the antagonism between winner and loser effects is capable of maintaining rank-order differences. Under bounded conditions, individual dominance values should not cluster near the upper or lower limits, as in the despotic and 'reverse despotic' hierarchies described previously. Beta-ranking individuals will always be kept in check by the alpha and second-to-last-ranking animals will be prevented from reaching the lower limit by continually dominating omega. However, when decreases in dominance values are bounded without concurrent maximum restrictions, the hierarchy again becomes despotic when both winner and loser effects operate (Dugatkin, 1997).

(6) Temporal decay

The effects of previous wins or losses may not persist indefinitely, but decay at a particular rate. A past experience often has less effect on subsequent fighting success than a recent experience (Hsu & Wolf, 1999; Cloutier & Newberry, 2000; Beacham, 2003). In Bonabeau *et al.*'s (1995, 1996) models, encounters between individuals were rare when group density was low. Under these circumstances, hierarchical differentiation was inhibited because individuals tended to 'forget' their previous social experience before encountering another groupmate. High densities promoted frequent aggressive interactions and reduced the probability of 'forgetting' previous social encounters before interacting again. Here, a clear social order materialised as individual dominance scores quickly differentiated. Hemelrijk (1999) arrived at a similar conclusion in her analyses of loose *versus*

dense groupings with infrequent aggressive interactions at low densities yielding weakly organised hierarchies. In the absence of density effects and when winner and loser effects decay at similar rates, the eventual hierarchies should resemble those where winner and loser effects operate simultaneously without decay. Experience decay may, however, slow the rate of hierarchical differentiation. No theoretical investigations have addressed the effects of asymmetrical decay rates on hierarchy formation (e.g. if loser effects decay slower than winner effects). Whether experience decay is modulated by neuroendocrine processes or by cognitive limitations, it is clear that 'forgetting' may play an important role in both the formation of hierarchies and the rate at which they differentiate.

(7) Interaction probabilities

The probability that two members of a group interact aggressively may influence how social experience is distributed among individuals and, as a consequence, how willing an animal is to engage in future interactions. In some theoretical models, interactions were assumed to occur at random (e.g. Theraulaz et al., 1991; Bonabeau et al., 1995) while others examined the relationship between particular interaction probabilities and the social and spatial characteristics of the group (Theraulaz et al., 1995; Bonabeau et al., 1996; Hemelrijk, 1998, 2000). Regardless of the interaction probabilities and, when both winner and loser effects operate, hierarchies had a clear rank-order (but see Theraulaz et al., 1995 and Bonabeau et al., 1996 for difficulties assigning intermediate ranks).

Dyadic interactions might influence the spatial arrangement of group members and subsequent interaction probabilities for specific contestants (e.g. Broom & Cannings, 2002). For instance, losers tend to move away from winners, but winners tend to remain at a site. If winning and losing have little effect on movement, spatial differentiation of the group is weak, if present at all, regardless of the interaction pattern implemented (Hemelrijk, 2000). When winner and loser effects on movements are strong, spatial centrality of dominants does emerge under certain circumstances, for instance, when individuals interact only if the probability of winning is high (see risk-sensitive, obligate attack, and ambiguity-reducing strategies in Hemelrijk, 1998, 2000). Strong winner and loser effects are a prerequisite for, but do not necessarily ensure, the emergence of spatial structure. Spatial differentiation feeds back on the social system in ways that may reinforce rank asymmetries and hierarchical stability (Hemelrijk, 1998, 2000), thus acting as an additional catalyst for the formation of linear dominance hierarchies. For instance, Beacham (2003) noted that experience effects could influence the spatial arrangement of animals in a way that facilitates the sequential development of dominance relationships, and as a consequence, strengthens linear hierarchies.

(8) Individual recognition

The ability of animals to distinguish familiar versus unfamiliar individuals plays an important role in modulating social interactions, for instance, behavioural decisions among shoaling fish (Griffiths, 2003) and competitive interactions in rodents (Petrulis, Weidner & Johnston, 2004). Individual recognition can reduce fighting costs in social situations where the probability of encountering the same opponent on a regular basis is high (Zayan, 1975; Temeles, 1994; Morris, Gass & Ryan, 1995; Johnsson, 1997; Pagel & Dawkins, 1997; O'Connor, Metcalfe & Taylor, 2000; Utne-Palm & Hart, 2000; Lopez & Martin, 2001). Furthermore, individual recognition might stabilize dominance hierarchies by reducing aggression among group members (e.g. Schjelderup-Ebbe, 1935; Allee, 1942; Guhl, 1968; Rowell, 1974; Karavanich & Atema, 1998; Hojesjo et al., 1998; Wiley et al., 1999).

While some authors have argued that individual or class (e.g. status signalling) recognition must play an integral role in linear hierarchy formation (Pagel & Dawkins, 1997), others have provided evidence that recognition strategies induce nonlinear hierarchies (e.g. Theraulaz et al., 1995; Bonabeau et al., 1996) or weaker hierarchies than those generated by winner and loser effects alone (Hemelrijk, 1996, 2000; Dugatkin & Earley, 2004). Nevertheless, small hierarchies are generally more linear than large hierarchies (e.g. see Chase, 1974). This pattern suggests that, under circumstances 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. In larger groups, hierarchy stability may rely more on recognition of relative rank or spatial distribution (Appleby, 1993; Pagel & Dawkins, 1997; Hemelrijk, 2000).

(9) Observer effects

As described in Section II (7), observing interactions between others may change a focal individual's assessment of the fighting ability of the monitored contestants. This raises the question of whether updating the fighting abilities of others rather than just of oneself has implications for hierarchy formation.

In a recent simulation model, Dugatkin (2001) demonstrated that when eavesdropping effects act in concert with winner and loser effects, linear hierarchies always emerge from a set of initially identical individuals. Due to the incorporation of eavesdropping effects, each individual's assessment of its own fighting ability was precisely the same as the way others perceived it, thereby promoting the development of a clear rank-order. Although some of Dugatkin's (2001) assumptions may not reflect natural circumstances (see Earley & Dugatkin, 2005), the model's predictions provide the impetus to investigate the joint effects of winning, losing, and eavesdropping on hierarchy formation. Indeed, an important study by Chase et al. (2003) indicated that the magnitude of experience effects, particularly loser effects, might change if obtained in the presence versus absence of additional individuals (possibly eavesdroppers).

Recognition of past opponents may also interact with information obtained through eavesdropping via transitive inference. If A loses to B and then witnesses C defeat B, A may also opt to avoid interacting with C. For animals that

are capable of transitive inference, the combination of individual recognition and eavesdropping may reduce errors in assessment of fighting ability and, in turn, further reduce rank-order ambiguity (e.g. Hogue, Beaugrand & Lague, 1996; Peake *et al.*, 2002). A recent modification of the Hawk-Dove game demonstrated that transitive inference strategies are evolutionarily stable when the costs of aggressive contests exceed, by some threshold level, the value of the contested resource (Nakamaru & Sasaki, 2003). In addition, transitive inference strategies promote the formation of linear dominance hierarchies whereas immediate inference strategies [see Section I (2) – The Sequential Assessment Model] do not. Eavesdropping may also modify hierarchy structure if watching fights alters aggression levels [e.g. priming; changes in hormone titres, see Section II (7); Oliveira *et al.*, 2001] toward individuals other than those that were observed insofar as altered aggression levels influence interaction probabilities, which might then feed back on hierarchy structure [see Section VI (7)].

(10) Summary

In the absence of other asymmetries that may influence contest outcome (e.g. size), winner and loser effects (and the properties thereof) may have major theoretical implications for hierarchy structure. Despite the vast number of testable predictions generated by the theoretical models described above (see Table 3), empirical studies on experience effects and hierarchy formation have lagged considerably behind. The most intuitive design for experiments to examine how experience effects influence the dynamics of an intact group is to eliminate all possible confounding asymmetries (size, residency, age, sex, etc.) and examine how social interactions occur through time (e.g. Goessmann *et al.*, 2000). Empirical studies and, particularly, conceptual models that aim to do this are often criticized for neglecting individual attributes (e.g. Slater, 1986). Admittedly, the 'jigsaw model' and related treatments do not account for variation in intrinsic characteristics, but several lines of empirical evidence have rejected the notion that individual differences *alone* can promote development of stable, linear hierarchies (Chase, 1986). In the absence of experience effects, linear hierarchies can theoretically emerge but, in the majority of cases, the rank-order does not correlate perfectly with fighting ability (Mesterton-Gibbons & Dugatkin, 1995). If rank correlates perfectly with one character or a suite of characters then a group of individuals with clear asymmetries in fighting ability should form precisely the same hierarchy regardless of the conditions under which they meet. Empirical evidence for such rank-order consistency is lacking, implicating contextual and dynamic factors as important in hierarchy formation (e.g. King, 1965; Bernstein & Gordon, 1980; Nelissen, 1985; Dugatkin, Alfieri & Moore, 1994; Verbeek *et al.*, 1999; Chase *et al.*, 2002, 2003).

Bonabeau *et al.* (1999) discovered that correlational models can generate the same predictions of hierarchy structure as those that employ experience effects and urged empiricists and theoreticians alike to accept the correlational model, which has fewer built-in assumptions, until more data are gathered on experience effects and hierarchy formation. Bonabeau *et al.* (1999) modelled the roles of experience and individual characteristics separately and did not examine their joint effects. If both asymmetries in intrinsic fighting ability and winner/loser effects are modelled simultaneously, however, an interesting interaction emerges. When differences in fighting abilities among individuals in a group are small, winner and loser effects drive hierarchy formation. When asymmetries in intrinsic fighting ability are large, winner and loser effects play a smaller role or need to be exceedingly strong to have an impact on dominance structure (Beaugrand & Cotnoir, 1996; Cloutier, Beaugrand & Lague, 1996; Beaugrand, 1997; Mesterton-Gibbons, 1999).

From these analyses, it appears as if a balance between social experience and initial individual differences influences hierarchical rank. Specifically, as intrinsic asymmetries between group members decrease, the ontogeny of a dominance order should depend increasingly on experience effects. The relative effects of intrinsic *versus* social factors may depend primarily on the initial composition of the group and can be experimentally tested. One can easily manipulate the degree of size asymmetries [or other intrinsic factor(s) that may bear on contest outcome] among group members, observe the hierarchical outcome, and assess winner and loser effects *via* observations of within-group dynamics.

The prospect for studying experience effects and hierarchy formation is immense. Although empirical analyses are still in their infancy, a solid theoretical framework provides a wealth of predictions that, with testing, may elucidate how winning and losing experiences affect rank-order dynamics. In viewing these effects from the perspective of the hierarchy, we may also begin to understand how the magnitude of winner or loser effects changes with social context (Chase *et al.*, 2003), the long-term fitness consequences of victory and defeat (e.g. reproductive opportunity), the dynamics of coalition formation in animal groups (Dugatkin, 1998; Johnstone & Dugatkin, 2000), or even how winner and loser effects might have evolved (e.g. Mesterton-Gibbons, 1999; see also Van Doorn, Hengeveld & Weissing, 2003 *a, b*).

VII. CONCLUSIONS

(1) Prior contest experience changes both behaviour in, and outcome of, subsequent contests. Earlier wins increase the chance of winning later; earlier losses decrease the chance of winning later. Losses often have more effect than wins. Experience can result either from observing or participating in contests. The effects are consistent with a changed perception of costs of a future contest.

(2) Taxa vary considerably in these effects, both in magnitude and duration (see Mackney & Hughes, 1995). Some, but not all, of this variation, results from methodological differences employed in the studies. Standardization of techniques would be valuable.

(3) Experience effects depend on neuroendocrine changes that influence behaviour which in turn influence contest outcomes.

(4) Neuroendocrine influences could be either learning and/or hormonal changes. Behavioural changes include a lowered probability of engaging in a contest or reacting with an attack after a loss and a greater probability of attacking after a win.

(5) Contest outcome changes as a result of experience are important in non-escalated contests, but of little to no importance in escalated contests, a result predicted by the sequential assessment model of contest behaviour.

(6) Quantitative models are proposed for integration of multiple experiences and predicting outcomes from different experience backgrounds. Integration is assumed to be additive among experiences with temporal decay, but could be modelled with more complex functions. Outcomes may follow one of four proposed models based on relative effects of minor and major differences in experiences of the contestants.

(7) Experience effects may play a role in formation of dominance hierarchies, but proposed hierarchical outcome depends on assumptions about the actual characteristics of the experience effects.

(8) Experience effects are only one of several influences on contest outcome. Others include size differences between contestants and residency effects.

(9) Future studies are needed on:

1. Behavioural changes in contests as a result of experience. These investigations would also provide insight into signalling during contests.

2. The neuroendocrine effects of experience. Much of the effect in many studies may be associated with hormonal changes, but the hormones involved as well as the pattern, magnitude, and decay of the hormonal effects currently are poorly understood. These studies should also consider the various possible sites of hormonal effects: e.g. hormone synthesis, release, and receptor sensitivities and densities.

3. How experiences differ in initial magnitude and decay of the effect. Does a difficult contest produce a different effect than an easy win and do taxa differ in predicable ways in the pattern of decay of the effects.

4. How multiple experiences are integrated through time by an individual. The model we propose is additive with a temporal decay function. But very limited evidence exists from studies in which individuals experience more than one prior contest.

5. The relative importance of major and minor differences in experience backgrounds to contest outcome. Does the experience effect depend on the perceived fighting abilities of the two rivals (F_i and F_j) and how different they have to be to generate a detectable change in the contest outcome.

6. The relative importance of other influences, e.g. residency size disparities, and potential benefit differences, on contest outcomes.

7. The role of experience effects in hierarchy formation.

8. The general applicability of the quantitative models to other behaviours, including mating and predator-prey interactions.

VIII. REFERENCES

ABBOTT, J. C., DUNBRACK, R. L. & ORR, C. D. (1985). The interaction of size & experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). *Behaviour* **92**, 241–253.

ABBOTT, D. H., KEVERNE, E. B., BERCOVITCH, F. B., SHIVELY, C. A., MENDOZA, S. P., SALTZMAN, W., SNOWDON, C. T., ZIEGLER, T. E., BANJEVIC, M., GARLAND, T. JR. & SAPOLSKY, R. M. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior* **43**, 67–82.

ADAMO, S. A. & HOY, R. R. (1995). Agonistic behaviour in male and female field crickets, *Gryllus bimaculatus*, and how behavioural context influences its expression. *Animal Behaviour* **49**, 1491–1501.

ADAMS, E. & CALDWELL, R. (1990). Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Animal Behavior* **39**, 706–716.

ALBERS, P. C. H. & DE VRIES, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour* **61**, 489–495.

ALEXANDER, R. D. (1961). Aggressive territoriality and sexual behaviour in field crickets (Orthoptera: Gryllidae). *Behaviour* **17**, 130–223.

ALLEE, W. C. (1942). Social dominance and subordination among vertebrates. Levels of integration in biological and social systems. *Biological Symposium* **8**, 139–162.

ALLEE, W. C., FOREMAN, D., BANKS, E. M. & HOLABIRD, C. M. (1955). Effects of an androgen on dominance and subordination in six common breeds of *Gallus gallus*. *Physiological Zoology* **28**, 89–115.

APPLEBY, M. C. (1993). How animals perceive a hierarchy: reactions to Freeman *et al. Animal Behaviour* **46**, 1232–1233.

ARMSTRONG, D. P. (1991). Aggressiveness of breeding territorial honeyeaters corresponds to seasonal changes in nectar availability. *Behavioral Ecology and Sociobiology* **29**, 103–111.

AUSTAD, S. N. (1983). A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Animal Behaviour* **31**, 59–73.

BAENNINGER, R. (1970). Visual reinforcement, habituation, and prior social experience of Siamese fighting fish. *Journal of Comparative Physiology and Psychology* **71**, 1–5.

BAKKER, TH. C. M., BRUIJN, E. & SEVENSTER, P. (1989). Asymmetrical effects of prior winning and losing on dominance in sticklebacks (*Gasterosteus aculeatus*). *Ethology* **82**, 224–229.

BAKKER, TH. C. M. & SEVENSTER, P. (1983). Determinants of dominance in male sticklebacks (*Gasterosteus aculeatus* L.). *Behaviour* **86**, 55–71.

BARCHAS, P. R. & MENDOZA, S. D. (1984). Emergent hierarchical relationships in rhesus macaques: an application of Chase's model. In *Social Hierarchies: Essays Toward a Sociophysiological Perspective* (ed. P. R. Barchas), pp. 81–95. Greenwood Press, Wesport, CT.

BARKI, A., HARPAZ, S. & KARPLUS, I. (1997). Contradictory asymmetries in body and weapon size, and assessment in fighting male prawns, *Macrobrachium rosenbergii*. *Aggressive Behavior* **23**, 81–91.

BARNARD, C. J. & BROWN, C. A. J. (1982). The effects of prior residence, competitive ability and food availability on the outcome of interactions between shrews (*Sorex araneus* L.). *Behavioral Ecology and Sociobiology* **10**, 307–312.

BARNARD, C. J. & BURK, T. (1979). Dominance hierarchies and the evolution of individual recognition. *Journal of theoretical Biology* **81**, 65–73.

BAUBE, C. L. (1997). Manipulations of signaling environment affect male competitive success in three-spined sticklebacks. *Animal Behaviour* **53**, 819–833.

BEACHAM, J. L. (1988). The relative importance of body size and aggressive experience as determinants of dominance in pumpkinseed sunfish, *Lepomis gibbosus*. *Animal Behaviour* **36**, 621–623.

BEACHAM, J. L. (2003). Models of dominance hierarchy formation: effects of prior experience and intrinsic traits. *Behaviour* **140**, 1275–1303.

BEACHAM, J. L. & NEWMAN, J. A. (1987). Social experience and the formation of dominance relationships in the pumpkinseed sunfish, *Lepomis gibbosus*. *Animal Behaviour* **35**, 1560–1562.

BEAUGRAND, J. P. (1997). Relative importance of initial individual differences, agonistic experience, and assessment accuracy during hierarchy formation: a simulation study. *Behavioural Processes* **41**, 177–192.

BEAUGRAND, J. P. & COTNOIR, P. A. (1996). The role of individual differences in the formation of triadic dominance orders of male green swordtail fish (*Xiphoporus helleri*). *Behavioural Processes* **38**, 287–296.

BEAUGRAND, J. P. & GOULET, C. (2000). Distinguishing kinds of prior dominance and subordination experiences in males of green swordtail fish (*Xiphophrorus helleri*). *Behavioural Processes* **50**, 131–142.

BEAUGRAND, J., GOULET, C. & PAYETTE, D. (1991). Outcome of dyadic conflict in male green swordtail fish, *Xiphophorus helleri*: effects of body size and prior dominance. *Animal Behaviour* **41**, 417–424.

BEAUGRAND, J. P., PAYETTE, D. & GOULET, C. (1996). Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*): interaction of body size, prior dominance/subordination experience, and prior residency. *Behaviour* **133**, 303–319.

BÉGIN, J., BEAUGRAND, J. P. & ZAYAN, R. (1996). Selecting dominants and subordinates at conflict outcome can confound the effects of prior dominance or subordination experience. *Behavioural Processes* **36**, 219–226.

BEKOFF, M. & DUGATKIN, L. A. (2000). Winner and loser effects and the development of dominance relationships in young coyotes: an integration of data and theory. *Evolutionary Ecology Research* **2**, 871–883.

BERGMAN, D. A., KOZLOWSKI, C. P., MCINTYRE, J. C., HUBER, R., DAWS, A. G. & MOORE, P. A. (2003). Temporal dynamics and communication of winner-effects in the crayfish, *Orconectes rusticus*. *Behaviour* **140**, 805–825.

BERNSTEIN, I. S. & GORDON, T. P. (1980). The social component of dominance relationships in rhesus monkeys (*Macaca mulatta*). *Animal Behaviour* **28**, 1033–1039.

BERNSTEIN, I. S., GORDON, T. P. & ROSE, R. M. (1983). The interaction of hormones, behavior, and social context in nonhuman primates. In *Hormones and Aggressive Behavior* (ed. B. B. Svare), pp. 535–561. Plenum, New York.

BEVAN, W., DAVES, W. F. & LEVY, G. W. (1960). The relation of castration, androgen therapy and pre-test fighting experience to competitive aggression in male C57 BL/10 mice. *Animal Behaviour* **8**, 6–12.

BOLYARD, K. J. & ROWLAND, W. J. (2000). The effects of spatial context and social experience on the territorial aggression of male threespine stickleback. *Behaviour* **137**, 845–864.

BONABEAU, E., THERAULAZ, G. & DENEUBOURG, J. L. (1995). Phase diagram of a model of self-organizing hierarchies. *Physica A* **217**, 373–392.

BONABEAU, E., THERAULAZ, G. & DENEUBOURG, J. L. (1996). Mathematical models of self-organizing hierarchies in animal societies. *Bulletin of Mathematical Biology* **58**, 661–719.

BONABEAU, E., THERAULAZ, G. & DENEUBOURG, J. L. (1999). Dominance orders in animal societies: the self-organization hypothesis revisited. *Bulletin of Mathematical Biology* **61**, 727–757.

BOOTH, A., SHELLEY, G., MAZUR, A., THARP, G. & KITTOK, R. (1989). Testosterone and winning and losing in human competition. *Hormones and Behavior* **23**, 556–571.

BOUTON, M. E. (1993). Context, time, and memory retrieval in the interference paradigms of Pavlovian learning. *Psychological Bulletin* **114**, 80–99.

BOUTON, M. E. (1994). Conditioning, remembering, and forgetting. *Journal of Experimental Psychology: Animal Behaviour Processes* **20**, 219–231.

BRICK, O. (1999). A test of the sequential assessment game: the effect of increased cost of sampling. *Behavioral Ecology* **10**, 726–732.

BRIFFA, M. & ELWOOD, R. W. (2001). Decision rules, energy metabolism and vigour of hermit-crab fights. *Proceedings of the Royal Society of London Series B* **268**, 1841–1848.

BRIFFA, M. & ELWOOD, R. W. (2002). Power of shell-rapping signals influence physiological costs and subsequent decisions during hermit crab fights. *Proceedings of the Royal Society of London Series B* **269**, 2331–2336.

BRIFFA, M. & ELWOOD, R. W. (2004). Use of energy reserves in fighting hermit crabs. *Proceedings Of The Royal Society Of London Series B-Biological Sciences* **271**, 373–379.

BROOM, M. & CANNINGS, C. (2002). Modeling dominance hierarchy formation as a multi-player game. *Journal of theoretical Biology* **219**, 397–413.

BROWN, C. & LALAND, K. N. (2003). Social learning in fishes: a review. *Fish and Fisheries* **4**, 280–288.

BROWN, M. J. F. & GORDON, D. M. (2000). How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant. *Behavioral Ecology and Sociobiology* **47**, 195–203.

BUCHANAN, K. L. (2000). Stress and the evolution of condition-dependent signals. *Trends in Ecology and Evolution* **15**, 156–160.

BUSH, R. & MOSTELLER, F. (1951). A mathematical model for simple learning. *Psychological Review* **58**, 313–323.

CARDWELL, J. R. & LILEY, N. R. (1991). Androgen control of social status in males of a wild population of stoplight parrotfish, *Sparisoma viride* (Scaridae). *Hormones and Behavior* **25**, 1–18.

CARPENTER, G. C. (1995). Modeling dominance: the influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetological Monographs* **9**, 88–101.

CASES, O., SEIF, I., GRIMSBY, J., GASPAR, P., CHEN, K., POURNIN, S., MULLER, U., AGUET, M., BABINET, C., SHIH, J. C. & DEMAEYER, E. (1995). Aggressive behavior and altered amounts of brain serotonin and norepinephrine in mice lacking MAOA. *Science* **268**, 1763–1766.

CASTO, J. M., NOLAN, V. JR. & KETTERSON, E. D. (2001). Steroid hormones and immune function: experimental studies in wild and captive dark-eyed juncos (*Junco hyemalis*). *American Naturalist* **157**, 408–420.

CASTRO, J. J. & CABALLERO, C. (1998). Dominance structure in small groups of juvenile white-seabream (*Diplodus sargus cadenati* de la Paz, Bauchot and Daget 1974). *Aggressive Behavior* **24**, 197–204.

CHAOULOFF, F. (1993). Physiopharmacological interactions between stress hormones and central serotonergic systems. *Brain Research Reviews* **18**, 1–32.

CHAPMAN, M. & KRAMER, D. (1996). Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. *Animal Behaviour* **52**, 83–94.

CHARNOV, E. L. (1976). Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**, 129–136.

CHASE, I. D. (1974). Models of hierarchy formation in animal societies. *Behavioral Science* **19**, 374–382.

CHASE, I. D. (1980). Social process and hierarchy formation in small groups: a comparative perspective. *American Sociological Review* **45**, 905–924.

CHASE, I. D. (1982*a*). Behavioral sequences during hierarchy formation in chickens. *Science* **216**, 439–440.

CHASE, I. D. (1982*b*). Dynamics of hierarchy formation: the sequential development of dominance relationships. *Behaviour* **80**, 218–240.

CHASE, I. D. (1985). The sequential analysis of aggressive acts during hierarchy formation: an application of the 'jigsaw puzzle' approach. *Animal Behaviour* **33**, 86–100.

CHASE, I. D. (1986). Individual differences and dominance hierarchies. *Animal Behaviour* **34**, 1264–1266.

CHASE, I. D., BARTOLOMEO, C. & DUGATKIN, L. A. (1994). Aggressive interactions and inter-contest interval: how long do winners keep winning? *Animal Behaviour* **48**, 393–400.

CHASE, I. D. & ROHWER, S. (1987). Two methods for quantifying the development of dominance hierarchies in large groups with applications to Harris' Sparrows. *Animal Behaviour* **35**, 1113–1128.

CHASE, I. D., TOVEY, C. & MURCH, P. (2003). Two's company, three's a crowd: differences in dominance relationships in isolated versus socially embedded pairs of fish. *Behaviour* **140**, 1193–1217.

CHASE, I. D., TOVEY, C., SPANGLER-MARTIN, D. & MANFREDONIA, M. (2002). Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proceedings of the National Academy of Science* **99**, 5744–5749.

CLEVELAND, A. (1999). Energetic costs of agonistic behavior in two herbivorous damselfishes (*Stegastes*). *Copeia* **1999**, 857–867.

CLOTFELTER, E. D. & PAOLINO, A. D. (2003). Bystanders to contests between conspecifics are primed for increased aggression in male fighting fish. *Animal Behaviour* **66**, 343–347.

CLOUTIER, S., BEAUGRAND, J. P. & LAGUE, P. C. (1996). The role of individual differences and patterns of resolution in the formation of dominance orders in domestic hen triads. *Behavioural Processes* **38**, 227–239.

CLOUTIER, S. & NEWBERRY, R. C. (2000). Recent social experience, body weight and initial patterns of attack predict the social status attained by unfamiliar hens in a new group. *Behaviour* **137**, 705–726.

CLUTTON-BROCK, T. H. & ALBON, S. D. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* **69**, 145–169.

CLUTTON-BROCK, T. H., ALBON, S. D., GIBSON, R. M. & FUINNESS, F. E. (1979). The logical stag: adaptive aspect of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour* **27**, 211–225.

COLLIAS, N. E. (1943). Statistical analysis of factors which make for success in initial encounters between hens. *American Naturalist* **77**, 519–538.

CONSTEN, D., BOGERD, J., KOMEN, J., LAMBERT, J. G. D. & GOOS, H. J. TH. (2001). Long-term cortisol treatment inhibits pubertal development in male common carp, *Cyprinus carpio* L. *Biology of Reproduction* **64**, 1063–1071.

CONSTEN, D., LAMBERT, J. G. D. & GOOS, H. J. TH. (2001). Cortisol affects testicular development in male common carp, *Cyrpinus carpio* L., but not via an effect on LH secretion. *Comparative Biochemistry and Physiology B* **129**, 671–677.

COWIE, R. J. (1977). Optimal foraging in great tits (*Parus major*). *Nature* **268**, 137–139.

CRESPI, B. J. (1986). Size assessment and alternative fighting tactics in *Elaphrothrips tuberculatus* (Insecta: Thysanoptera). *Animal Behaviour* **34**, 1324–1335.

CRISTOL, D. A. (1995). The coat-tail effect in merged flocks of dark-eyed juncos: social status depends on familiarity. *Animal Behaviour* **50**, 151–159.

CRISTOL, D. A., NOLAN, V. JR. & KETTERSON, E. D. (1990). Effect of prior residence on dominance status of dark-eyed juncos, Junco hyemalis. *Animal Behaviour* **40**, 580–586.

CROWLEY, P. H., GILLETT, S. & LAWTON, J. H. (1988). Contests between larval damselflies: empirical steps toward a better ESS model. *Animal Behaviour* **36**, 1496–1510.

DAVIDSON, S. M. & WILKINSON, G. S. (2004). Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. *Animal Behaviour* **67**, 883–891.

DAVIES, N. & HALLIDAY, T. (1978). Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* **274**, 683–685.

DAVIS, E. S. & MARLER, C. A. (2003). The progesterone challenge: steroid hormone changes following a simulated territorial intrusion in female *Peromyscus californicus*. *Hormones and Behavior* **44**, 185–198.

DAWS, A. G., GRILLS, J., KONZEN, K. & MOORE, P. A. (2002). Previous experiences alter the outcome of aggressive interactions between males in the crayfish, *Procambrus clarkii*. *Marine and Freshwater Behavior and Physiology* **35**, 139–148.

DEGHETT, V. J. (1975). A factor influencing aggression in adult mice: witnessing aggression when young. *Behavioral Biology* **13**, 291–300.

DEVENPORT, L. D. (1998). Spontaneous recovery without interference: why remembering is adaptive. *Animal Learning and Behavior* **26**, 172–181.

DEVENPORT, L. D. & DEVENPORT, J. A. (1994). Time-dependent averaging of foraging information in least chipmunks and golden-mantled ground squirrels. *Animal Behaviour* **47**, 787–802.

DICKINSON, J. (1992). Scramble competition polygyny in the milkweed leaf beetle: combat, mobility, and the importance of being there. *Behavioral Ecology* **3**, 32–41.

DINAN, T. G. (1996). Serotonin & the regulation of the hypothalamic-pituitary-adrenal axis function. *Life Sciences* **58**, 1683–1694.

DODSON, G. N. & SCHWAAB, A. T. (2001). Body size, leg autonomy, and prior experience as factors in the fighting success of male crab spiders, *Misumenoides formosipes*. *Journal of Insect Behavior* **14**, 841–855.

DOWDS, B. M. & ELWOOD, R. W. (1985). Shell wars II: the influence of relative size on decisions made during hermit crab shell fights. *Animal Behaviour* **33**, 649–656.

DRAUD, M. & LYNCH, P. A. E. (2002). Asymmetric contests for breeding sites between monogamous pairs of convict cichlids

(*Archocentrus nigrofasciatum*, Cichlidae): pair experience pays. *Behaviour* **139**, 861–873.

DRUMMOND, H. & CANALES, C. (1998). Dominance between booby nestlings involves winner and loser effects. *Animal Behaviour* **55**, 1669–1676.

DRUMMOND, H. & OSORNO, J. L. (1992). Training siblings to be submissive losers: dominance between booby nestlings. *Animal Behaviour* **44**, 881–893.

DRUMMOND, H., TORRES, R. & KRISHNAN, V. V. (2003). Buffered development: resilience after aggressive subordination in infancy. *American Naturalist* **161**, 794–807.

DUFTY, A. M., COLBERT, J. & MOLLER, A. P. (2002). Hormones, development plasticity and adaptation. *Trends in Ecology & Evolution* **17**, 190–196.

DUGATKIN, L. A. (1997). Winner effects, loser effects, assessment strategies and the structure of dominance hierarchies. *Behavioral Ecology* **8**, 583–587.

DUGATKIN, L. A. (1998). A model of coalition formation in animals. *Proceedings of the Royal Society of London Series B* **265**, 2121–2125.

DUGATKIN, L. A. (2001). Bystander effects and the structure of dominance hierarchies. *Behavioral Ecology* **12**, 348–352.

DUGATKIN, L. A., ALFIERI, M. S. & MOORE, A. J. (1994). Can dominance hierarchies be replicated? Form re-form experiments using the cockroach (*Nauphoeta cinerea*). *Ethology* **97**, 94–102.

DUGATKIN, L. A. & BIEDERMAN, L. (1991). Balancing asymmetries in resource holding power and resource value in the pumpkinseed fish. *Animal Behaviour* **42**, 691–692.

DUGATKIN, L. A. & DRUEN, M. (2004). The social implications of winner and loser effects. *Proceedings of the Royal Society of London Series B* (Suppl.) **271**, S488–S489.

DUGATKIN, L. A. & EARLEY, R. L. (2003). Group fusion: the impact of winner, loser, and bystander effects on hierarchy formation in large groups. *Behavioral Ecology* **14**, 367–373.

DUGATKIN, L. A. & EARLEY, R. L. (2004). Individual recognition, dominance hierarchies, and winner and loser effects. *Proceedings of the Royal Society of London Series B* **271**, 1537–1540.

DUGATKIN, L. A. & OHLSEN, S. (1990). Contrasting asymmetries in value expectation and resource holding power: effects on attack behaviour and dominance in the pumpkinseed sunfish, *Lepomis gibbosus*. *Animal Behaviour* **39**, 802–804.

EARLEY, R. L., ATTUM, O. & EASON, P. (2002). Varanid combat: perspectives from game theory. *Amphibia-Reptilia* **23**, 469–485.

EARLEY, R. L., BLUMER, L. S. & GROBER, M. S. (2004). The gall of subordination: changes in gallbladder function associated with social stress. *Proceedings of the Royal Society of London Series B* **271**, 7–13.

EARLEY, R. L., DRUEN, M. & DUGATKIN, L. A. (2005) Watching fights does not alter a bystander's response toward naïve conspecifics in male green swordtail fish (*Xiphophorus helleri*). *Animal Behaviour* **69**, 1139–1145.

EARLEY, R. L. & DUGATKIN, L. A. (2002). Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking. *Proceedings of the Royal Society of London Series B* **269**, 943–952.

EARLEY, R. L. & DUGATKIN, L. A. (2005). Fighting, mating and networking: pillars of poeciliid sociality. In *Animal Communication Networks* (ed. P. K. McGregor), pp. 84–113. Cambridge University, Cambridge.

EARLEY, R. L., TINSLEY, M. & DUGATKIN, L. A. (2003). To see or not to see: does previewing a future opponent affect the contest behavior of green swordtail males (*Xiphophorus helleri*)? *Naturwissenschaften* **90**, 226–230.

ECKERT, C. G. & WEATHERHEAD, P. J. (1987). Owners, floaters and competitive asymmetries among territorial red-winged blackbirds. *Animal Behaviour* **35**, 1317–1323.

EDWARDS, D. H. & KRAVITZ, E. A. (1997). Serotonin, social status and aggression. *Current Opinion in Neurobiology* **7**, 812–819.

ELIAS, M. (1981). Serum cortisol, testosterone, and testosterone-binding globulin responses to competitive fighting in human males. *Aggressive Behavior* **7**, 215–224.

ELLIS, L. (1995). Dominance and reproductive success among non-human animals: a cross-species comparison. *Ethology and Sociobiology* **16**, 257–333.

ELOFSSON, U. O. E., MAYER, I., DAMSGARD, B. & WINBERG, S. (2000). Intermale competition in sexually mature Arctic charr: effects on brain monoamines, endocrine stress responses, sex hormone levels, and behavior. *General and Comparative Endocrinology* **118**, 450–460.

ENGLUND, G. & OLSSON, T. I. (1990). Fighting and assessment in the net-spinning caddis larva *Arctopsyche ladogensis*: a test of the sequential assessment game. *Animal Behaviour* **39**, 55–62.

ENGLUND, G. & OTTO, C. (1991). Effects of ownership status, weight asymmetry and case fit on the outcome of case contests in two populations of *Agrypnia pagetana* (Trichoptera: Phryganeidae) larvae. *Behavior Ecology and Sociobiology* **29**, 113–120.

ENQUIST, M. & LEIMAR, O. (1983). Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of theoretical Biology* **102**, 387–410.

ENQUIST, M. & LEIMAR, O. (1987). Evolution of fighting behavior: The effect of variation in resource value. *Journal of theoretical Biology* **127**, 187–205.

ENQUIST, M., LEIMAR, O., LJUNGBERG, T., MALLNER, Y. & SEFERDAHL, N. (1990). A test of the sequential assessment game: fighting in the cichlid fish *Nannocara anomala*. *Animal Behaviour* **40**, 1–14.

EWALD, P. W. (1985). Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Animal Behaviour* **33**, 705–719.

EWALD, P. W. & CARPENTER, F. L. (1978). Territorial responses to energy manipulations in the Anna hummingbird. *Oecologia* **31**, 277–292.

EWING, L. S. & EWING, A. W. (1973). Correlates of subordinate behaviour in the cockroach, *Nauphoeta Cinerea*. *Animal Behaviour* **21**, 571–578.

FERNALD, R. D. (1976). The effect of testosterone on the behavior and coloration of adult male cichlid fish (*Haplochromis burtoni*, Gunther). *Hormone Research* **7**, 172–178.

FLÜGGE, G., KRAMER, M., RENSING, S. & FUCHS, E. (1998). 5HT(1A)-receptors and behaviour under chronic stress: selective counteraction by testosterone. *European Journal of Neuroscience* **10**, 2685–2693.

FORKMAN, B. & HASKELL, M. J. (2004). The maintenance of stable dominance hierarchies and the pattern of aggression: support for the suppression hypothesis. *Ethology* **110**, 737–744.

FOX, H. E., WHITE, S. A., KAO, M. H. F. & FERNALD, R. D. (1997). Stress and dominance in a social fish. *Journal of Neuroscience* **17**, 6463–6469.

FRANCIS, R. C. (1983). Experiential effects on agnostic behavior in the paradise fish, *Macropodus opercularis*. *Behaviour* **85**, 292–313.

FRANCK, D. & RIBOWSKI, A. (1987). Influences of prior agonistic experiences on aggression measures in the male swordtail (*Xiphophorus helleri*). *Behaviour* **103**, 217–240.

FRANCK, D. & RIBOWSKI, A. (1989). Escalating fights for rank-order position between male swordtails (*Xiphophorus helleri*): effects of

prior rank-order experience and information transfer. *Behavioral Ecology and Sociobiology* **24**, 133–143.

FREEMAN, L. C., FREEMAN, S. C. & ROMNEY, A. K. (1992). The implications of social structure for dominance hierarchies in red deer, *Cervus elaphus* L. *Animal Behaviour* **44**, 239–245.

FREY, D. F. & MILLER, R. J. (1972). The establishment of dominance relationships in the blue gourami *Trichogaster trichopterus* (Pallus). *Behaviour* **42**, 8–62.

FULLER, R. W. (1990). Serotonin receptors and neuroendocrine responses. *Neuropsychopharmacology* **3**, 495–502.

GINSBURG, B. & ALLEE, W. C. (1942). Some effects of conditioning on social dominance and subordination in inbred strains of mice. *Physiological Zoology* **15**, 485–506.

GOESSMANN, C., HEMELRIJK, C. & HUBER, R. (2000). The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. *Behavioral Ecology and Sociobiology* **48**, 418–428.

GOMEZ-LAPLAZA, L. M. & MORGAN, E. (2000). Laboratory studies of the effects of short-term isolation on aggressive behaviour in fish. *Marine Freshwater Behavior and Physiology* **33**, 63–102.

GOODSON, J. L. (1998). Territorial aggression and dawn song are modulated by septal vasotocin and vasoactive intestinal polypeptide in male field sparrows (*Spizella pusilla*). *Hormones and Behavior* **34**, 67–77.

GOTTFRIED, B., ANDREWS, K. & HAUG, M. (1985). Breeding robins and nest predators: effect of predator type and defense strategy on initial vocalization patterns. *Wilson Bulletin* **97**, 183–190.

GOULET, C. & BEAUGRAND, J. P. (unpublished data). Relations between dominance status, agonistic intensity in mirror tests, and subsequent aggressive levels in winner and losers of dyads of male Green swordtail fish (*Xiphophorus helleri*). http://cogprints.ecs.soton.ac.uk/

GOYMANN, W. & WINGFIELD, J. C. (2004). Allostatic load, social status and stress hormones: the costs of social status matter. *Animal Behaviour* **67**, 591–602.

GRANTNER, A. & TABORSKY, M. (1998). The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: Cichlidae). *Journal of Comparative Physiology B* **186**, 427–433.

GRIFFITHS, S. W. (2003). Learned recognition of conspecifics by fishes. *Fish and Fisheries* **4**, 256–268.

GUHL, A. M. (1968). Social inertia and social stability in chickens. *Animal Behaviour* **16**, 219–232.

HACK, M. A. (1997 *a*). Assessment strategies in the contests of male crickets, *Acheta domesticus* (L). *Animal Behaviour* **53**, 733–747.

HACK, M. A. (1997 *b*). The energetic costs of fighting in the house cricket, *Acheta domesticus* L. *Behavioral Ecology* **8**, 28–36.

HACK, M. A., THOMPSON, D. J. & FERNANDES, D. M. (1997). Fighting in males of the autumn spider, *Metellina segmentata*: effects of relative body size, prior residency and female value on contest outcome and duration. *Ethology* **103**, 488–498.

HALLER, J. (1991). Muscle metabolic changes during the first six hours of cohabitation in pairs of male *Betta splendens*. *Physiology and Behavior* **49**, 1301–1303.

HALLER, J. (1992). Group size modifies the patterns and muscle carbohydrate effects of aggression in *Betta splendens*. *Physiology and Behavior* **52**, 287–290.

HALLER, J., KIEM, D. T. & MAKARA, G. B. (1996). The physiology of social conflict in rats: what is particularly stressful? *Behavioral Neuroscience* **110**, 353–359.

HALLER, J. & WITTENBERGER, C. (1988). Biochemical energetics of hierarchy formation in *Betta splendens*. *Physiology and Behavior* **43**, 447–450.

HALPERIN, J. R. P. & DUNHAM, D. W. (1993). Increased aggressiveness after brief social isolation of adult fish: a connectionist model which organizes this literature. *Behavioural Processes* **28**, 123–144.

HALPERIN, J. R. P., DUNHAM, D. W. & YE, S. (1992). Social isolation increases social display after priming in *Betta splendens* but decreases aggressive readiness. *Behavioural Processes* **28**, 13–32.

HALPERIN, J. R. P., GIRI, T. & DUNHAM, D. W. (1997). Different aggressive behaviours are exaggerated by facing vs. broadside subliminal stimuli shown to socially isolated Siamese fighting fish, *Betta splendens*. *Behavioural Processes* **40**, 1–11.

HALPERIN, J. R. P., GIRI, T., ELLIOTT, J. & DUNHAM, D. W. (1998). Consequences of hyper-aggressiveness in Siamese fighting fish: cheaters seldom prosper. *Animal Behaviour* **55**, 87–96.

HAMMERSTEIN, P. & PARKER, G. A. (1982). The asymmetric war of attrition. *Journal of Theoretical Biology* **96**, 647–682.

HANNES, R. P., FRANCK, D. & LIEMANN, F. (1984). Effects of rank-order fights on whole-body and blood concentrations of androgens and corticosteroids in the male swordtail (*Xiphophorus helleri*). *Zeitschrift fur Tierpsychologie* **65**, 53–65.

HARDING, C. F. (1983). Hormonal influences on avian aggressive behavior. In *Hormones and Aggressive Behavior* (ed. B. B. Svare), pp. 435–467. Plenum, New York.

HARLEY, C. B. (1981). Learning the evolutionary stable strategy. *Journal of Theoretical Biology* **89**, 611–633.

HEMELRIJK, C. K. (1996). Dominance interactions, spatial dynamics and emergent reciprocity in a virtual world. In *From Animals to Animats 4: Proceedings of the 4th International Conference on Simulation of Adaptive Behavior* (eds. P. Maes, M. J. Mataric, J. A. Meyer, J. Pollack and S. W. Wilson), pp. 545–552. MIT Press, Cambridge, MA.

HEMELRIJK, C. K. (1998). Risk sensitive and ambiguity reducing dominance interactions in a virtual laboratory. In *From Animals to Animats 5: Proceedings of the 5th International Conference on Simulation of Adaptive Behavior* (eds. R. Pfeifer, B. Blumberg, J. A. Meyer and S. W. Wilson), pp. 255–262. MIT Press, Cambridge, MA.

HEMELRIJK, C. K. (1999). An individual-oriented model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society of London Series B* **166**, 361–369.

HEMELRIJK, C. K. (2000). Towards the integration of social dominance and spatial structure. *Animal Behaviour* **5**, 1035–1048.

HEMELRIJK, C. K. (2002). Self-organization and natural selection in the evolution of complex despotic societies. *Biological Bulletin* **202**, 283–289.

HIGBY, M., BEULIG, A. & DWYER, J. (1991). Exogenous testosterone and social experience each enhance the development of aggressive behavior in *Cyprinodon variegatus*. *Aggressive Behavior* **17**, 229–239.

HOEFLER, C. D. (2002). Is contest experience a trump card? The interaction of residency status, experience, and body size on fighting success in *Misumenoides formisopes* (Aranea: Thomisidae). *Journal of Insect Behavior* **15**, 779–790.

HOFMANN, H. A. & STEVENSON, P. A. (2000). Flight restores fight in crickets. *Nature* **403**, 613.

HOGEWEG, P. & HESPER, B. (1983). The ontogeny of the interaction structure in bumblebee colonies: a MIRROR model. *Behavioral Ecology and Sociobiology* **12**, 271–283.

HOGEWEG, P. & HESPER, B. (1985). Socioinformatic processes: MIRROR Modelling methodology. *Journal of Theoretical Biology* **113**, 311–330.

HOGLUND, E., BALM, P. H. M. & WINBERG, S. (2000). Skin darkening, a potential social signal in subordinate Arctic charr (*Salvelinus alpinus*): the regulatory role of brain monoamines and pro-opiomelanocortin-derived peptides. *Journal of Experimental Biology* **203**, 1711–1721.

HOGLUND, E., BALM, P. H. M. & WINBERG, S. (2002). Stimulatory and inhibitory effects of 5-HT1A receptors on adrenocorticotropic hormone and cortisol secretion in a teleost fish, the Arctic charr (*Salvelinus alpinus*). *Neuroscience Letters* **324**, 193–196.

HOGUE, M. E., BEAUGRAND, J. P. & LAGUE, P. C. (1996). Coherent use of information by hens observing their former dominant defeating or being defeated by a stranger. *Behavioural Processes* **38**, 241–252.

HOJESJO, J., JOHNSSON, J., PETERSSON, E. & JARVI, T. (1998). The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). *Behavioral Ecology* **9**, 445–451.

HOLLIS, K. L. (1984). The biological function of Pavlovian conditioning: the best defense is a good offense. *Journal of Experimental Psychology* **10**, 413–425.

HOLLIS, K. L., DUMAS, M. J., SINGH, P. & FACKELMAN, P. (1995). Pavlovian conditioning of aggressive behavior in blue gourami fish (*Trichogaster trichopterus*): winners become winners and losers stay losers. *Journal of Comparative Psychology* **109**, 125–133.

HOPKINS, P. O. (1987). Behavioural dominance: some elementary probabilistic considerations and their behavioural implications. *Behavioural Processes* **15**, 211–231.

HOUSTON, A. I., KACELNIK, A. & MCNAMARA, J. (1982). Some learning rules for acquired information. In *Functional Ontogeny* (ed. D. J. McFarlane), pp. 140–191. Pitman, Boston, MA.

HOUTSMULLER, E. J. & SLOB, A. K. (1990). Masculinization and defeminization of female rats by males located caudally in the uterus. *Physiology and Behavior* **48**, 555–560.

HSU, Y. & WOLF, L. L. (1999). The winner and loser effect: integrating multiple experiences. *Animal Behaviour* **57**, 903–910.

HSU, Y. & WOLF, L. L. (2001). The winner and loser effect: what fighting behaviours are influenced? *Animal Behaviour* **61**, 777–786.

HUBER, R. & DELAGO, A. (1998). Serotonin alters decisions to withdraw in fighting crayfish, *Astacus astacus*: the motivational concept revisited. *Journal of Comparative Physiology A* **182**, 573–583.

HUBER, R., SMITH, K., DELAGO, A., ISAKSSON, K. & KRAVITZ, E. A. (1997). Serotonin and aggressive motivation in crustaceans: altering the decision to retreat. *Proceedings of the National Academy of Science USA* **94**, 5939–5942.

HUHMAN, K. L., MOORE, T. O., FERRIS, C. F., MOUGEY, E. H. & MEYERHOFF, J. L. (1991). Acute and repeated exposure to social conflict in male golden hamsters: increases in plasma POMC-peptides and cortisol and decreases in plasma testosterone. *Hormones and Behavior* **25**, 206–216.

HUHMAN, K. L., MOORE, T. O., MOUGEY, E. H. & MEYERHOFF, J. L. (1992). Hormonal responses to fighting in hamsters: separation of physical and psychological causes. *Physiology and Behavior* **51**, 1083–1086.

HUHMAN, K. L., SOLOMON, M. B., JANICKI, M., HARMON, A. C., LIN, S. M., ISRAEL, J. E. & JASNOW, A. M. (2003). Conditioned defeat in male and female Syrian hamsters. *Hormones and Behavior* **44**, 293–299.

JACKSON, W. M. (1991). Why do winners keep winning? *Behavioral Ecology and Sociobiology* **25**, 429–436.

JACKSON, W. M. & WINNEGRAD, R. L. (1988). Linearity in dominance hierarchies: a second look at the individual attributes model. *Animal Behaviour* **36**, 1237–1240.

JAGER, E. & SEGEL, L. A. (1992). On the distribution of dominance in populations of social organisms. *SIAM Journal of Applied Mathematics* **52**, 1442–1468.

JAKOBSSON, S., BRICK, O. & KULLBERG, C. (1995). Escalated fighting behaviour incurs increased predation risk. *Animal Behaviour* **49**, 235–239.

JASNOW, A. M., BANKS, M. C., OWENS, E. C. & HUHMAN, K. L. (1999). Differential effects of two corticotropin-releasing factor antagonists on conditioned defeat in male Syrian hamsters (*Mesocricetus auratus*). *Brain Research* **846**, 122–128.

JASNOW, A. M., DRAZEN, D. L., HUHMAN, K. L., NELSON, R. J. & DEMAS, G. E. (2001). Acute and chronic social defeat suppresses humoral immunity of male Syrian hamsters (*Mesocricetus auratus*). *Hormones and Behavior* **40**, 428–433.

JASNOW, A. M. & HUHMAN, K. L. (2001). Activation of GABAA receptors in the amygdala blocks the acquisition and expression of conditioned defeat in Syrian hamsters. *Brain Research* **920**, 142–150.

JOHNSSON, J. I. (1997). Individual recognition affects aggression and dominance relations in rainbow trout, *Oncorhynchus mykiss*. *Ethology* **103**, 267–282.

JOHNSTONE, R. A. (2001). Eavesdropping and animal conflict. *Proceedings of the National Academy of Science USA* **98**, 9177–9180.

JOHNSTONE, R. A. & DUGATKIN, L. A. (2000). Coalition formation in animals and the nature of winner and loser effects. *Proceedings of the Royal Society of London Series B* **267**, 17–21.

JUST, W. & MORRIS, M. R. (2003). The Napolean complex: why smaller males pick fights. *Evolutionary Ecology* **17**, 509–522.

KACELNIK, A., KREBS, J. R. & ENS, B. (1987). Foraging in a changing environment: an experiment with starlings (*Sturnus vulgaris*). In *Quantitative Analysis of Behavior. Vol. 6: Foraging* (eds. M. L. Commons, A. Kacelnik and S. J. Shettleworth), pp. 63–87. Lawrence Erlbaum, Hillsdale, New Jersey.

KAHN, M. W. (1951). The effect of severe defeat at various age levels on the aggressive behavior of mice. *Journal of Genetic Psychology* **79**, 117–130.

KARAVANICH, C. & ATEMA, J. (1998). Individual recognition and memory in lobster dominance. *Animal Behaviour* **56**, 1553–1560.

KAWASHIMA, I. (2004). Sexual dimorphism and agonistic behavior of *Exechesops leucopis* (Jordan) (Coleoptera: Anthribidae: Anthribinae). *Coleopterists Bulletin* **58**, 77–83.

KENNEDY, M. & GRAY, R. D. (1994). Agonistic interactions and the distribution of foraging organisms – individual costs and social information. *Ethology* **96**, 155–165.

KHAZRAIE, K. & CAMPAN, M. (1999). The role of prior agonistic experience in dominance relationships in male crickets *Gryllus bimaculatus* (Orthoptera: Gryllidae). *Behavioural Processes* **44**, 341–348.

KIM, T. & ZUK, M. (2000). The effects of age and previous experience on social rank in female red junglefowl, *Gallus gallus spadiceus*. *Animal Behaviour* **60**, 239–244.

KING, M. G. (1965). The effects of social context on dominance capacity of domestic hens. *Animal Behaviour* **13**, 132–133.

KITCHEN, D. M., SEYFARTH, R. M., FISCHER, J. & CHENEY, D. L. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* **53**, 374–384.

KNAPP, R. & MOORE, M. C. (1996). Male morphs in tree lizards, *Urosaurus ornatus*, have different delayed hormonal responses to aggressive encounters. *Animal Behaviour* **52**, 1045–1055.

KOOPS, M. A. & ABRAHAMS, M. V. (2003). Integrating the roles of information and competitive ability on the spatial distribution of social foragers. *American Naturalist* **161**, 586–600.

KREBS, J. R. & DAVIES, N. B. (eds.) (1997). *Behavioural Ecology, An Evolutionary Approach*, 4th edn. Blackwell Science, Inc., Malden, MA.

KUDRYAVTSEVA, N. N. (2000). An experimental approach to the study of learned aggression. *Aggressive Behavior* **26**, 241–256.

LADICH, F. (1998). Sound characteristics and outcome of contests in male croaking gouramis (Teleostei). *Ethology* **104**, 517–529.

LANDAU, H. G. (1951). On dominance relations and the structure of animal societies: II. Some effects of possible social factors. *Bulletin of Mathematical Biophysics* **13**, 245–262.

LARSON, E. T. & SUMMERS, C. H. (2001). Serotonin reverses dominant social status. *Behavioural Brain Research* **121**, 95–102.

LEBOEUF, B. J. & PETERSON, R. S. (1969). Social status and mating activity in elephant seals. *Science* **163**, 91–93.

LEIMAR, O. & ENQUIST, M. (1984). Effects of asymmetries in the owner-intruder conflicts. *Journal of theoretical Biology* **111**, 475–491.

LESHNER, A. I. (1983). The hormonal responses to competition and their behavioral significance. In *Hormones and Aggressive Behavior* (ed. B. B. Svare), pp. 393–404. Plenum, New York.

LILEY, N. R. & KROON, F. J. (1995). Male dominance, plasma hormone concentrations, and availability of milt in male rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Zoology* **73**, 826–836.

LINDSTROM, K. (1992). The effect of resource holding potential, nest size and information about resource quality on the outcome of intruder-owner conflicts in the sand goby. *Behavior Ecology and Sociobiology* **30**, 53–58.

LOPEZ, P. & MARTIN, J. (2001). Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*. *Behavioral Ecology and Sociobiology* **49**, 111–116.

LUCAS, L. R., CELEN, Z., TAMASHIRO, K. L. K., BLANCHARD, R. J., BLANCHARD, D. C., MARKHAM, C., SAKAI, R. R. & MCEWEN, B. S. (2004). Repeated exposure to social stress has long-term effects on indirect markers of dopaminergic activity in brain regions associated with motivated behavior. *Neuroscience* **12**, 449–457.

MACKNEY, P. A. & HUGHES, R. N. (1995). Foraging behaviour and memory window in sticklebacks. *Behaviour* **132**, 1241–1253.

MARDEN, J. H. & WAAGE, J. K. (1990). Escalated damselfly territorial contests are energetic wars of attrition. *Animal Behaviour* **39**, 954–959.

MARLER, C. A. & MOORE, M. C. (1988). Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behavioral Ecology and Sociobiology* **23**, 21–26.

MARTIN, F., BEAUGRAND, J. P. & LAGUE, P. C. (1997*a*). The role of hen's weight and recent experience on dyadic conflict outcome. *Behavioural Processes* **41**, 139–150.

MARTIN, F., BEAUGRAND, J. P. & LAGUE, P. C. (1997*b*). The role of recent experience and weight on hen's agonistic behaviour during dyadic conflict resolution. *Behavioural Processes* **41**, 159–170.

MARTÍNEZ, M., SALVADOR, A. & SIMON, V. M. (1994). Behavioral changes over several successful agonistic encounters between male mice: effects of type of 'standard opponent.' *Aggressive Behavior* **20**, 441–451.

MAYNARD, SMITH, J. (1974). The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology* **47**, 209–221.

MAYNARD, SMITH, J. & PARKER, G. A. (1976). The logic of asymmetric contests. *Animal Behaviour* **24**, 159–175.

MAYNARD, SMITH, J. & PRICE, G. R. (1973). The logic of animal conflict. *Nature* **246**, 15–18.

MAZUR, J. E. (1995). Development of preference and spontaneous recovery in choice behavior with concurrent variable-interval schedules. *Animal Learning and Behavior* **23**, 93–103.

MAZUR, J. E. (1996). Past experience, recency, and spontaneous recovery in choice behavior. *Animal Learning and Behavior* **24**, 1–10.

MCDONALD, A. L., HEIMSTRA, N. W. & DAMKOT, D. K. (1968). Social modification of agonistic behaviour in fish. *Animal Behaviour* **16**, 437–441.

MCGREGOR, P. K. & DABELSTEEN, T. (1996). Communication Networks. In *Ecology and Evolution of Acoustic Communication in Birds* (eds. D. E. Kroodsma and E. H. Miller), pp. 409–425. Cornell University Press, Ithaca, NY.

MCGREGOR, P. K., DABELSTEEN, T. & HOLLAND, J. (1997). Eavesdropping in a territorial songbird communication network: preliminary results. *Bioacoustics* **8**: 253–254.

MCGREGOR, P. K., PEAKE, T. M. & LAMPE, H. M. (2001). Fighting fish *Betta splendens* extract relative information from apparent interactions: what happens when what you see is not what you get. *Animal Behaviour* **62**, 1059–1065.

MCPEEK, M. A. & CROWLEY, P. H. (1987). The effects of density and relative size on the aggressive behaviour, movement, and feeding of damselfly larvae (Odonata: Coenagrionidae). *Animal Behaviour* **35**, 1051–1061.

MENDOZA, S. P. & BARCHAS, P. R. (1983). Behavioral processes leading to linear status hierarchies following group formation in rhesus monkeys. *Journal of Human Evolution* **12**, 185–192.

MESTERTON-GIBBONS, M. (1999). On the evolution of pure winner and loser effects: a game-theoretic model. *Bulletin of Mathematical Biology* **61**, 1151–1186.

MESTERTON-GIBBONS, M. & ADAMS, E. S. (1998). Animal contest as evolutionary games. *American Scientist* **86**, 334–341.

MESTERTON-GIBBONS, M. & DUGATKIN, L. A. (1995). Toward a theory of dominance hierarchies: effects of assessment, group size and variation in fighting ability. *Behavioral Ecology* **6**, 416–423.

MESTERTON-GIBBONS, M., MARDEN, J. H. & DUGATKIN, L. A. (1996). On wars of attrition without assessment. *Journal of theoretical Biology* **181**, 65–83.

MIKLÓSI, A., HALLER, J. & CSANYI, V. (1997). Learning about the opponent during aggressive encounters in paradise fish (*Macropodus opercularis* L.): when it takes place? *Behavioural Processes* **40**, 97–105.

MOORE, A. J., CICCONE, W. J. & BREED, M. D. (1988). The influence of social experience on the behavior of male cockroaches, *Nauphoeta cinerea. Journal of Insect Behavior* **1**, 157–168.

MORETZ, J. A. (2003). Aggression and RHP in the Northern swordtail fish, *Xiphophorus cortezi*: the relationship between size and contest dynamics in male-male competition. *Ethology* **109**, 995–1008.

MORRIS, M. R., GASS, L. & RYAN, M. J. (1995). Assessment and individual recognition of opponents in the pygmy swordtails *Xiphophorus nigrensis* and *X. multilineatus. Behavioral Ecology and Sociobiology* **37**, 303–310.

MOUSSEAU, T. A. & FOX, C. W. (eds.) (1998). *Maternal effects as adaptations*. Oxford University Press, New York.

MULLER, M. N. & WRANGHAM, R. W. (2004). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology* **55**, 332–340.

NAGUIB, M., FITCHEL, C. & TODT, D. (1999). Nightingales respond more strongly to vocal leaders of simulated dyadic interactions. *Proceedings of the Royal Society of London Series B* **266**, 537–542.

NAGUIB, M. & TODT, D. (1997). Effects of dyadic vocal interactions on other conspecific receivers in nightingales. *Animal Behaviour* **54**, 1535–1543.

NAKAMARU, M. & SASAKI, A. (2003). Can transitive inference evolve in animals playing the hawk-dove game? *Journal of theoretical biology* **222**, 461–470.

NEAT, F. C., TAYLOR, A. C. & HUNTINGFORD, F. A. (1998). Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. *Animal Behaviour* **55**, 875–882.

NEAT, F. C. & MAYER, I. (1999). Plasma concentrations of sex steroids and fighting in male *Tilapia zilii*. *Journal of Fish Biology* **54**, 695–697.

NEIL, S. (1984). Contests for space in breeding *Cichlasoma meeki*: the use of increased apparent size displays. *Behaviour* **87**, 283–297.

NELISSEN, M. H. J. (1985). Structure of the dominance hierarchy and dominance determining 'group factors' in *Melanochromis auratus*. *Behaviour* **94**, 85–107.

NELISSEN, M. H. J. & ANDRIES, S. (1988). Does previous experience affect the ranking of cichlid fish in a dominance hierarchy? *Annals of the Royal Zoological Society of Belgium* **118**, 41–50.

O'CONNOR, K. I., METCALFE, N. B. & TAYLOR, A. C. (2000). Familiarity influences body darkening in territorial disputes between juvenile salmon. *Animal Behaviour* **59**, 1095–1101.

OLIVEIRA, R. C. & ALMADA, V. C. (1996). Dominance hierarchies and social structure in captive groups of the Mozambique tilapia *Oreochromis mossambicus* (Teleostei Cichlidae). *Ethology, Ecology & Evolution* **8**, 39–55.

OLIVEIRA, R. F., ALMADA, V. C. & CANARIO, A. V. M. (1996). Social modulation of sex steroid concentrations in the urine of male cichlid fish *Oreochromis mossambicus*. *Hormones and Behavior* **30**, 2–12.

OLIVEIRA, R. F., HIRSCHENHAUSER, K., CARNEIRO, L. A. & CANARIO, A. V. M. (2002). Social modulation of androgen levels in male teleost fish. *Comparative Biochemistry and Physiology B* **132**, 203–215.

OLIVEIRA, R. F., LOPES, M., CARNEIRO, L. A. & CANARIO, A. V. M. (2001). Watching fights raises fish hormone levels. *Nature* **409**, 475.

OLIVEIRA, R. F., McGREGOR, P. K. & LATRUFFE, C. (1998). Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proceedings of the Royal Society of London Series B* **265**, 1045–1049.

OLSSON, M. (1992). Contests success in relation to size and residency in male sand lizards, *Lacerta agilis*. *Animal Behaviour* **44**, 386–388.

OLSSON, M. (1993). Contests success and mate guarding in male sand lizards, *Lacerta agilis*. *Animal Behaviour* **46**, 408–409.

OTRONEN, M. (1990). The effect of prior experience on the outcome of fights in the burying beetle, *Nicrophorus humator*. *Animal Behaviour* **40**, 980–1004.

OVERLI, O., HARRIS, C. A. & WINBERG, S. (1999a). Short-term effects of fights for social dominance and the establishment of dominant-subordinate relationships on brain monoamines and cortisol in rainbow trout. *Brain Behavior and Evolution* **54**, 263–275.

OVERLI, O., KORZAN, W. J., HOGLUND, E., WINBERG, S., BOLLIG, H., WATT, M., FORSTER, G. L., BARTON, B. A., OVERLI, E., RENNER, K. J. & SUMMERS, C. H. (2004). Stress coping style predicts aggression and social dominance in rainbow trout. *Hormones and Behavior* **45**, 235–241.

OVERLI, O., OLSEN, R. E., LOVIK, F. & RINGO, E. (1999b). Dominance hierarchies in Arctic charr, *Salvelinus alpinus L.*: differential cortisol profiles of dominant and subordinate individuals after handling stress. *Aquaculture Research* **30**, 259–264.

PAGEL, M. & DAWKINS, M. S. (1997). Peck orders and group size in laying hens: 'future contracts' for non-aggression. *Behavioural Processes* **40**, 13–25.

PANKHURST, N. W. & VAN DER KRAAK, G. (2000). Evidence that acute stress inhibits ovarian steroidogenesis in rainbow trout in vivo through the action of cortisol. *General and Comparative Endocrinology* **117**, 225–237.

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

PATNAIK, B. K., MAHAPATRO, N. & JENA, B. S. (1994). Aging in fishes. *Gerontology* **40**, 113–132.

PAYNE, R. J. H. (1998). Gradually escalating fights and displays: the cumulative assessment model. *Animal Behaviour* **56**, 651–662.

PAYNE, R. J. H. & PAGEL, M. (1997). Why do animals repeat displays? *Animal Behaviour* **54**, 109–119.

PEAKE, T. M., TERRY, A. M. R., McGREGOR, P. K. & DABELSTEEN, T. (2001). Male great tits eavesdrop on simulate male-to-male vocal interactions. *Proceedings of the Royal Society of London Series B* **268**, 1183–1187.

PEAKE, T. M., TERRY, A. M. R., McGREGOR, P. K. & DABELSTEEN, T. (2002). Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proceedings of the Royal Society of London Series B* **269**, 1925–1929.

PETRIE, M. (1988). Intraspecific variation in structures that display competitive ability: large animals invest relatively more. *Animal Behaviour* **36**, 1174–1179.

PETRULIS, A., WEIDNER, M. & JOHNSTON, R. E. (2004). Recognition of competitors by male golden hamsters. *Physiology & Behavior* **81**, 629–638.

POLAK, M. (1994). Large-size advantage and assessment of resource holding potential in male *Polistes fuscatus* (F.) (Hymenoptera: Vespidae). *Animal Behaviour* **48**, 121–124.

POPP, J. W. (1988). Effects of experience on agonistic behavior among American goldfinches. *Behavioural Processes* **16**, 11–19.

PRATT, A. E., McLAIN, D. K. & LATHROP, G. R. (2003). The assessment game in sand fiddler crab contests for breeding burrows. *Animal Behaviour* **65**, 945–955.

PRYKE, S. R., ANDERSSON, S., LAWES, M. J. & PIPER, S. E. (2002). Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. *Behavioral Ecology* **13**, 622–631.

RAMOS-FERNANDEZ, G., NUNEZ-DE LA MORA, A., WINGFIELD, J. C. & DRUMMOND, H. (2000). Endocrine correlates of dominance in chicks of the blue-footed booby (*Sula nebouxii*): testing the challenge hypothesis. *Ethology Ecology and Evolution* **12**, 27–34.

RATNER, S. C. (1961). Effect of learning to be submissive on status in the peck order of domestic fowl. *Animal Behaviour* **9**, 34–37.

REBY, D. & McCOMB, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour* **65**, 519–530.

RIECHERT, S. E. (1979). Games spiders play. II: resource assessment strategies. *Behavioral Ecology and Sociobiology* **6**, 121–128.

RIECHERT, S. E. (1984). Games spiders play. III: cues underlying context-associated changes in agonistic behaviour. *Animal Behaviour* **32**, 1–15.

RIECHERT, S. E. (1986). Spider fights as a test of evolutionary game theory. *American Scientist* **74**, 604–610.

ROBERTSON, A. G. M. (1986). Male territoriality, fighting and assessment of fighting ability in the Australian frog *Uperoleia rugosa*. *Animal Behaviour* **34**, 763–772.

ROSENBERG, R. H. & ENQUIST, M. (1991). Contest behaviour in Weidemeyer's admiral butterfly *Limenitis weidemeyerii* (Nymphalidae): the effect of size and residency. *Animal Behaviour* **42**, 805–811.

ROVERO, F., HUGHES, R. N., WHITELEY, N. M. & CHELAZZI, G. (2000). Estimating the energetic cost of fighting in shore crabs by noninvasive monitoring of heartbeat rate. *Animal Behaviour* **59**, 705–713.

ROWELL, T. E. (1974). The concept of social dominance. *Behavioral Biology* **11**, 131–154.

ROWLAND, W. J. (1989). The ethological basis of mate choice in male threespine sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour* **38**, 112–120.

RUIZ-DE-LA-TORRE, J. L. & MANTECA, X. (1999). Effects of testosterone on aggressive behaviour after social mixing in male lambs. *Physiology and Behavior* **68**, 109–113.

SAKAKURA, Y., TAGAWA, M. & TSUKAMOTO, K. (1998). Whole-body cortisol concentrations and ontogeny of aggressive behavior in yellowtail (Seriola quinqueradiata Temminck and Schlegel; Carangidae). *General and Comparative Endocrinology* **109**, 286–292.

SANDS, J. & CREEL, S. (2004). Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. *Animal Behaviour* **67**, 387–396.

SAUDOU, F., AMARA, D. A., DIERICH, A., LEMEUR, M., RAMBOZ, S., SEGU, L., BUHOT, M.-C. & HEN, R. (1994). Enhanced aggressive behavior in mice lacking 5-HT1B receptor. *Science* **265**, 1875–1878.

SAVAGE, K. E., HUNT, J., JENNIONS, M. D. & BROOKS, R. (2005). Male attractiveness covaries with fighting ability but not with prior fight outcome in house crickets. *Behavioral Ecology* **16**, 196–200.

SAVINO, J. F. & KOSITCH, M. J. (2000). Aggressive and foraging behavioral interactions among ruffe. *Environmental Biology of Fishes* **57**, 337–345.

SCHJELDERUP-EBBE, T. (1922). Beitrage zur Sozialpsychologie des Haushuhns. *Zeitschrift fur Psychologie* **88**, 225–252.

SCHJELDERUP-EBBE, T. (1935). Social behavior of birds. In *Handbook of Social Psychology* (ed. C. Murchison), pp. 947–972. Clark University Press, Worcester, MA.

SCHUETT, G. W. (1997). Body size and agonistic experience affect dominance and mating success in male copperheads. *Animal Behaviour* **54**, 213–224.

SCHUETT, G. W. & GROBER, M. S. (2000). Post-fight levels of plasma lactate and corticosterone in male copperheads, *Agkistrodon contortrix* (Serpentes, Viperidae): differences between winners and losers. *Physiology and Behavior* **71**, 335–341.

SCHUETT, G. W., HARLOW, H. J., ROSE, J. D., VAN KIRK, E. A. & MURDOCH, W. J. (1996). Levels of plasma corticosterone and testosterone in male copperheads (*Agkistrodon contortrix*) following staged fights. *Hormones and Behavior* **30**, 60–68.

SCOTT, J. P. & FREDERICSON, E. (1951). The causes of fighting in mice and rats. *Physiological Zoology* **24**, 273–309.

SEWARD, J. P. (1946). Aggressive behavior in the rat. IV. Submission as determined by conditioning, extinction, and disuse. *Journal of Comparative Psychology* **39**, 51–76.

SILVERIN, B. (1980). Effects of long-acting testosterone treatment on free-living pied flycatchers, *Ficedula hypoleuca*, during the breeding period. *Animal Behaviour* **28**, 906–912.

SILVERIN, B., BAILLIEN, M. & BALTHAZART, J. (2004). Territorial aggression, circulating levels of testosterone, and brain aromatase activity in free-living pied flycatchers. *Hormones and Behavior* **45**, 225–234.

SIMMONS, L. W. (1986). Inter-male competition and mating success in the field cricket, *Gryllus bimaculatus* (De Geer). *Animal Behaviour* **34**, 567–579.

SKVORETZ, J., FAUST, K. & FARARO, T. J. (1996). Social structure, networks, and E-state structuralism models. *Journal of Mathematical Sociology* **21**, 57–76.

SLATER, P. J. B. (1986). Individual differences and dominance hierarchies. *Animal Behaviour* **34**, 1264–1265.

SLATER, C. H. & SCHRECK, C. B. (1993). Testosterone alters the immune response of Chinook salmon *Oncorhynchus tshawytscha*. *General and Comparative Endocrinology* **89**, 291–298.

SLOMAN, K. A., GILMOUR, K. M., TAYLOR, A. C. & METCALFE, N. B. (2000). Physiological effects of dominance hierarchies within groups of brown trout, *Salmo trutta*, held under simulated natural conditions. *Fish Physiology and Biochemistry* **22**, 11–20.

SLOMAN, K. A., METCALFE, N. B., TAYLOR, A. C. & GILMOUR, K. M. (2001). Plasma cortisol concentrations before and after social stress in rainbow trout and brown trout. *Physiological and Biochemical Zoology* **74**, 383–389.

SMITH, T. (1990). Resource use by bill morphs of an African finch: evidence for intraspecific competition. *Ecology* **71**, 1246–1257.

SNEDDON, L. U., HUNTINGFORD, F. A. & TAYLOR, A. C. (1998). Impact of an ecological factor on the costs of resource acquisition: fighting and metabolic physiology of crabs. *Functional Ecology* **12**, 808–815.

SNEDDON, L. U., TAYLOR, A. C. & HUNTINGFORD, F. A. (1999). Metabolic consequences of agonistic behaviour: crab fights in declining oxygen tensions. *Animal Behaviour* **57**, 353–363.

SNEDDON, L. U., TAYLOR, A. C., HUNTINGFORD, F. A. & WATSON, D. G. (2000). Agonistic behaviour and biogenic amines in shore crabs *Carcinus maenus*. *Journal of Experimental Biology* **203**, 537–545.

STAMPS, J. A. (2003). Behavioural processes affecting development: Tinbergen's fourth question comes of age. *Animal Behaviour* **66**, 1–13.

STAMPS, J. A. & KRISHNAN, V. V. (1994a). Territory acquisition in lizards: I. First encounters. *Animal Behaviour* **47**, 1375–1385.

STAMPS, J. A. & KRISHNAN, V. V. (1994b). Territory acquisition in lizards: II. Establishing social and spatial relationships. *Animal Behaviour* **47**, 1387–1400.

STAMPS, J. A. & KRISHNAN, V. V. (1998). Territory acquisition in lizards: IV. Obtaining high status and exclusive home ranges. *Animal Behaviour* **55**, 461–472.

SUMMERS, C. H. (2001). Mechanisms for quick & variable responses. *Brain Behavior and Evolution* **57**, 283–292.

SUMMERS, C. H., KAMPSHOFF, J. L., RONAN, P. J., LOWRY, C. A., PRESTBO, A. A., KORZAN, W. J. & RENNER, K. J. (2003a). Monoaminergic activity in subregions of the raphe nuclei elicited by prior stress and the neuropeptide corticotropin-releasing factor. *Journal of Neuroendocrinology* **15**, 1122–1133.

SUMMERS, C. H., LARSON, E. T., RONAN, P. J., HOFMANN, P. M., EMERSON, A. J. & RENNER, K. J. (2000). Serotonergic responses

to corticosterone and testosterone in the limbic system. *General and Comparative Endocrinology* **117**, 151–159.

SUMMERS, C. H., LARSON, E. T., SUMMERS, T. R., RENNER, K. J. & GREENBERG, N. (1998). Regional and temporal separation of serotonergic activity mediating social stress. *Neuroscience* **87**, 489–496.

SUMMERS, C. H., SUMMERS, T. R., MOORE, M. C., KORZAN, W. J., WOODLEY, S. K., RONAN, P. J., HOGLUND, E., WATT, M. J. & GREENBERG, N. (2003*b*). Temporal patterns of limbic mono-amine and plasma corticosterone response during social stress. *Neuroscience* **116**, 553–563.

TAYLOR, P. W. & ELWOOD, R. W. (2003). The mismeasure of animal contests. *Animal Behaviour* **65**, 1195–1202.

TAYLOR, P. W., HASSON, O. & CLARK, D. L. (2001). Initiation and resolution of jumping spider contests: roles for size, proximity, and early detection of rivals. *Behavioral Ecology and Sociobiology* **50**, 403–413.

TEMELES, E. J. (1994). The role of neighbors in territorial systems: when are they 'dear enemies'? *Animal Behaviour* **47**, 339–350.

THERAULAZ, G., BONABEAU, E. & DENEUBOURG, J. L. (1995). Self-organization of hierarchies in animal societies: the case of the primitively eusocial wasp *Polistes dominulus Christ. Journal of theoretical Biology* **174**, 313–323.

THERAULAZ, G., GOSS, S., GERVET, J. & DENEUBOURG, J. L. (1991). Task differentiation in *Polistes* wasp colonies: a model for self-organizing groups of robots. In *From animals to animats: Proceedings of the 1st International Conference on Simulation of Adaptive Behavior* (eds. J. A. Meyer and S. W. Wilson), pp. 346–355. MIT Press, Cambridge, MA.

THINES, G. & HEUTS, B. (1968). The effect of submissive experi-ences on dominance and aggressive behaviour of *Xiphophorus* (Pisces, Poeciliidae). *Zeitschrift fur Tierpsychologie* **25**, 139–154.

THORPE, K. E., TAYLOR, A. C. & HUNTINGFORD, F. A. (1995). How costly is fighting? Physiological effects of sustained exercise and fighting in swimming crabs, *Necora puber* (L.) (Brachyura, Portunidae). *Animal Behaviour* **50**, 1657–1666.

TRAINOR, B. C., BIRD, I. M. & MARLER, C. A. (2004). Opposing hormonal mechanisms of aggression revealed through short-lived testosterone manipulations and multiple winning experi-ences. *Hormones and Behavior* **45**, 115–121.

TURNER, G. F. (1994). The fighting tactics of male mouthbrooding cichlids: the effects of size and residency. *Animal Behaviour* **47**, 655–662.

UTNE-PALM, A. C. & HART, P. J. B. (2000). The effects of fam-iliarity on competitive interactions between threespined stickle-backs. *Oikos* **91**, 225–232.

VAN DE POLL, N. E., DE JONGE, F., VAN OYEN, H. G. & VAN PELT, J. (1982). Aggressive behaviour in rats: effects of winning or losing on subsequent aggressive interactions. *Behavioural Processes* **7**, 143–155.

VAN DOORN, G. S., HENGEVELD, G. M. & WEISSING, F. J. (2003*a*). The evolution of social dominance I: two-player models. *Behaviour* **140**, 1305–1332.

VAN DOORN, G. S., HENGEVELD, G. M. & WEISSING, F. J. (2003*b*). The evolution of social dominance II: multi-player models. *Behaviour* **140**, 1333–1358.

VERBEEK, M. E. M., DE GOEDE, P., DRENT, P. J. & WIEPKEMA, P. R. (1999). Individual behavioural characteristics and dominance in aviary groups of great tits. *Behaviour* **136**, 23–48.

VERRELL, P. (1986). Wrestling in the red-spotted newt (*Notophthalmus viridescens*): resource value and contestant

asymmetry determine contest duration and outcome. *Animal Behaviour* **34**, 398–402.

VILLARS, T. A. (1983). Hormones and aggressive behavior in teleost fishes. In *Hormones and Aggressive Behavior* (ed. B. B. Svare), pp. 407–433. Plenum Press, New York.

VOM SAAL, F. S. (1979). Prenatal exposure to androgen influences morphology and aggressive behavior of male and female mice. *Hormones and Behavior* **12**, 1–11.

WAGNER, W. (1989*a*). Graded aggressive signals in Blanchard's cricket frog: vocal responses to opponent proximity and size. *Animal Behaviour* **38**, 1025–1038.

WAGNER, W. (1989*b*). Fighting, assessment, and frequency alter-ation in Blanchard's cricket frog. *Behavior Ecology and Sociobiology* **25**, 429–436.

WAGNER, W. (1992). Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. *Animal Behaviour* **44**, 449–462.

WALLEN, K. & WOJCIECHOWSKI-METZLAR, C. I. (1985). Social con-ditioning and dominance in male *Betta splendens*. *Behavioural Processes* **11**, 181–188.

WARBURTON, K. (2003). Learning of foraging skills by fish. *Fish and Fisheries* **4**, 203–215.

WEIGER, W. A. (1997). Serotonergic modulation of behaviour: a phylogenetic review. *Biological Reviews* **72**, 61–95.

WEINGRILL, T., GRAY, D. A., BARRETT, L. & HENZI, S. P. (2004). Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmen-tal factors. *Hormones and Behavior* **45**, 259–269.

WELLS, M. S. (1988). Effects of body size and resource value on fighting behaviour in a jumping spider. *Animal Behaviour* **36**, 321–326.

WEST-EBERHARD, M. J. (1989). Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* **20**, 249–278.

WHITE, K. G. (2001). Forgetting functions. *Animal Learning and Behavior* **29**, 193–207.

WHITEHOUSE, M. A. (1997). Experience influence male-male con-tests in the spider *Argyrodes antipodiana* (Theridiidae: Araneae). *Animal Behaviour* **53**, 913–923.

WILEY, R. H. (1990). Prior-residence and coat-tail effects in domi-nance relationship of male dark-eyed juncos, *Junco hyemalis*. *Animal Behaviour* **40**, 587–596.

WILEY, R. H., STEADMAN, L., CHADWICK, L. & WOLLERMAN, L. (1999). Social inertia in white-throated sparrows results from recognition of opponents. *Animal Behaviour* **57**, 453–463.

WINBERG, S. & LEPAGE, O. (1998). Elevation of brain 5-HT activity, POMC expression, and plasma cortisol in socially subordinate rainbow trout. *American Journal of Physiology* **274** (*Regulatory, Integrative and Comparative Physiology*) **43**, R645–R654.

WINBERG, S. & NILSSON, G. E. (1993*a*). Roles of brain monoamine neurotransmitters in agonistic behaviour and stress reactions, with particular reference to fish. *Comparative Biochemistry and Physiology* **106C**, 597–614.

WINBERG, S. & NILSSON, G. E. (1993*b*). Time course of changes in brain serotonergic activity and brain tryptophan levels in domi-nant and subordinate juvenile Arctic charr. *Journal of Experimental Biology* **179**, 181–195.

WINBERG, S., NILSSON, A., HYLLAND, P., SODERSTOM, V. & NILSSON, G. E. (1997). Serotonin as a regulator of hypothalamic-pituitary-interrenal activity in teleost fish. *Neuroscience Letters* **230**, 113–116.

WINBERG, S., NILSSON, G. E. & OLSEN, K. H. (1991). Social rank and brain levels of monoamines and monoamine metabolites in

Arctic charr, *Salvelinus alpinus* (L.). *Journal of Comparative Physiology A* **168**, 241–246.

WINBERG, S., NILSSON, G. E. & OLSEN, K. H. (1992). Changes in brain serotonergic activity during hierarchic behavior in Arctic charr (*Salvelinus alpinus* L.) are socially induced. *Journal of Comparative Physiology A* **170**, 93–99.

WOMMACK, J. C. & DELVILLE, Y. (2003). Repeated social stress and the development of agonistic behavior: individual differences in coping responses in male golden hamsters. *Physiology and Behavior* **80**, 303–308.

WOOTTON, R. J. (1976). *The Biology of Sticklebacks*. Academic Press, London.

YANG, E. J. & WILCZYNSKI, W. (2002). Relationships between hormones and aggressive behavior in green anole lizards: an analysis using structural equation modeling. *Hormones and Behavior* **42**, 192–205.

YASUKAWA, K. & BICK, E. I. (1983). Dominance hierarchies in dark-eyed juncos (*Junco hyemalis*): a test of a game-theory model. *Animal Behaviour* **31**, 439–448.

YEH, S. R., FRICKE, R. A. & EDWARDS, D. H. (1996). The effect of social experience on serotonergic modulation of the escape circuit of crayfish. *Science* **271**, 366–369.

YEH, S. R., MUSOLF, B. E. & EDWARDS, D. H. (1997). Neuronal adaptations to changes in social dominance status of crayfish. *Journal of Neuroscience* **17**, 697–708.

YOUNG, K. A. (2003) Evolution of fighting behavior under asymmetric competition: an experimental test with juvenile salmonids. *Behavioral Ecology* **14**, 127–134.

ZAMUDIO, K. R., HUEY, R. B. & CRILL, W. D. (1995). Bigger isn't always better: body size, developmental and parental temperature and male territorial success in *Drosophila melanogaster*. *Animal Behaviour* **49**, 671–677.

ZAYAN, R. C. (1975). Territorial defense and individual recognition in Xiphophorus (Pisces, Poeciliidae). *Behaviour* **52**, 266–312.

ZELENA, D., HALLER, J., HALASZ, J. & MAKARA, G. B. (1999). Social stress of variable intensity: physiological and behavioral consequences. *Brain Research Bulletin* **48**, 297–302.

ZIELINSKI, W. J. & VANDENBERGH, J. G. (1993). Testosterone and competitive ability in male house mice, *Mus musculus*: laboratory and field studies. *Animal Behaviour* **45**, 873–891.

ZUCKER, N. & MURRAY, L. (1996). Determinants of dominance in the tree lizard *Urosaurus ornatus*: the relative importance of mass, previous experience and coloration. *Ethology* **102**, 812–825.