

PREVIOUS EXPERIENCES ALTER THE OUTCOME OF AGGRESSIVE INTERACTIONS BETWEEN MALES IN THE CRAYFISH, *PROCAMBARUS CLARKII*

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Various measures of size have been associated with increased likelihood of winning such agonistic encounters between decapod crustaceans. Recent social experience, in the form of ‘winner’ or ‘loser’ effects, has also been shown to alter the outcome of encounters between size-matched individuals. This study further explores the importance of social experience in crustacean agonistic encounters. Crayfish, *Procambarus clarkii*, of different size classes were given a series of winning or losing experiences to determine whether this would affect their likelihood of success in subsequent fights. Recent wins or losses in a series of fights did alter the likelihood of an individual winning a subsequent encounter, despite an apparent disparity in size between opponents that would otherwise serve as an accurate predictor of the outcome.

Keywords: Winner effect; Aggression; Social behavior; Hierarchy

INTRODUCTION

Given the importance of agonistic encounters and aggressive behavior in determining dominance status, either within a dyad or in the larger context of a dominance hierarchy, much attention has been given to the factors that influence an individual’s likelihood of winning a bout and achieving dominance. Such factors include the size, age, and sex of the individual (Allen and Aspey, 1986) and the behavioral strategies they employ (Verbeek *et al.*, 1999). Also, the social context in which an altercation takes place can affect the outcome (Bernstein and Gordon, 1980), as can prior residence in the contest location by one of the protagonists (Figler and Einhorn, 1983; Evans and Shehadi-Moacdieh, 1988). As important as these factors are, theoretical studies suggest that they are not necessary for dominance to be established. Mathematical models show that populations of initially identical individuals will form stable dominance hierarchies

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in situations devoid of individual differences and social context, provided the results of an interaction affect the likely outcome of future interactions (Bonabeau *et al.*, 1995; Theraulaz *et al.*, 1995; Dugatkin, 1997). Such winner and loser effects, whereby winners become more likely to win subsequent fights and losers tend to suffer further losses, have been demonstrated many times in fish (Frey and Miller, 1972; Francis, 1983; Beacham and Newman, 1987; Beacham, 1988; Beaugrand *et al.*, 1991; Chase *et al.*, 1994; Hsu and Wolf, 1999) and also in birds (Jackson, 1991). These theoretical and empirical studies suggest that dominance hierarchies are the collective result of dyadic dominance relationships formed during agonistic interactions.

Agonistic interactions between clawed decapod crustaceans have attracted particular attention due to their prominent and potentially lethal weaponry. The most common factor in determining the outcome of an encounter between decapod crustaceans is the relative size of the opponents (Bovbjerg, 1953, 1956; Rubenstein and Hazlett, 1974; Ranta and Lindström, 1992, 1993; Figler *et al.*, 1995a; Pavey and Fielder, 1996), even when these differences are small and the opponents are otherwise closely matched in size (Vye *et al.*, 1997). These findings are consistent with game theory models in which protagonists assess possible size asymmetries and use this information in deciding whether to escalate an encounter or to retreat (Hack, 1997; Whitehouse, 1997; Nowbahari *et al.*, 1999; Moya-Laraño and Wise, 2000). Studies have also shown that relative claw size plays an important role in determining the outcome of an encounter (Barki *et al.*, 1991, 1997; Garvey and Stein, 1993; Rutherford *et al.*, 1995; Sneddon *et al.*, 1997). Prior residence by one of the opponents (Peeke *et al.*, 1995), molt stage (Tamm and Cobb, 1978), reproductive status (Figler *et al.*, 1995b; Mello *et al.*, 1999), behavioral strategies employed by the contestants (Guiasu and Dunham, 1997), and previous social experience (Dunham, 1972; Rubenstein and Hazlett, 1974) have also been shown to contribute to the outcome of an agonistic interaction between clawed decapods.

A recent study provided evidence of winner and loser effects in the formation of dominance relationships in crayfish (Goessmann *et al.*, 2000). Given the strong bias towards physical determinants of dominance, particularly in decapod crustaceans, the aim of the present study using freshwater crayfish, *Procambarus clarkii*, was to determine whether controlled social experience, in the form of winning and losing events, could reverse the outcome of agonistic encounters as predicted by the size of the contestants.

MATERIALS AND METHODS

Study Animals

Freshwater crayfish, *P. clarkii*, were obtained from Carolina Biological Supply Company and housed separately in 38 L aquaria equipped with under-gravel filters at a water temperature of $20 \pm 1^\circ\text{C}$. Animals were kept on a 12 : 12 h light : dark cycle and fed 3–5 g of frozen fish flesh three times a week. Animals were isolated for a minimum of two weeks before the experiment commenced. In our experience, this length of isolation is sufficient to allow individuals to be considered socially naïve for the purposes of this study. Prior to use in experiments, and after each fight, individuals were inspected for missing appendages. Animals without injuries or missing append-

ages were sexed and given identification marks using paint on the dorsal carapace. Weights and measures of chelae and carapace size were also taken. No animal lost a limb during agonistic encounters staged during the experiment.

Experimental Design

A group of 24 male crayfish was divided into four size classes according to mass. The size classes consisted of 6 Large (L) crayfish (35.1–56.6 g; chelae length 51–85 mm), 6 Medium-Large (M-L) crayfish (21.1–31.0 g; chelae length 39–49 mm), 6 Medium-Small (M-S) crayfish (15.7–20.7 g; chelae length 35–40 mm), and 6 Small (S) crayfish (12.7–14.8 g; chelae length 32–42 mm).

Agonistic encounters between pairs of individuals were staged in a 20 L aquarium (interaction tank) filled with 13 L de-chlorinated water. Encounters were filmed against a white background using a Panasonic WV-C1350 video camera mounted 1–1.5 m from the interaction tank and recorded on a Panasonic A6-1980 VCR. Pairs of crayfish were placed into opposite ends of the interaction tank, which were separated by an opaque divider, and allowed to acclimate for 20 min. After the acclimation period, the divider was removed and the animals were allowed to interact for 30 min or until one individual retreated from the other several times by performing tailflips.

The retreating individual was deemed the 'loser' of the encounter, and its opponent was deemed the 'winner'. In the few instances where neither individual performed a tailflip, analysis of the video record was used to determine the winner and loser of the bout. The individual that retreated most often from advances made by its opponent was deemed the 'loser'. These individuals characteristically adopted submissive postures, retreating slowly backwards, holding their bodies low against the substrate with their tail tightly curled beneath their abdomen. Aggressive postures on the other hand, such as raising the body from the substrate, or raising and spreading the chelae (meral spread), were most common in the individual that was least likely to retreat from its opponent. This individual was deemed the 'winner'. At the conclusion of each trial the crayfish were returned to their holding tanks. The interaction tank was rinsed three times with de-ionised water and twice with tap water, and then refilled with de-chlorinated water for the next trial. Individual crayfish was not used in more than two trials on the same day, with at least 6 h between trials.

Preconditioning Fights

Fights were staged between individuals from the M-L and M-S size classes such that all possible pairwise contests were performed (Fig. 1). Each crayfish participated in two trials a day for three days. The 6 individuals that lost the majority of these encounters (4 or more out of 6 encounters) were classified as 'losers', and the 6 individuals that won the most encounters were classified as 'winners'. The outcome of these fights agreed with predictions based on size differences.

Conditioning Fights

During conditioning fights individuals were paired with opponents of the size class most likely to reverse their recent status as either a winner or a loser as determined by the preconditioning fights. To this effect, the M-L individuals ('winners') were

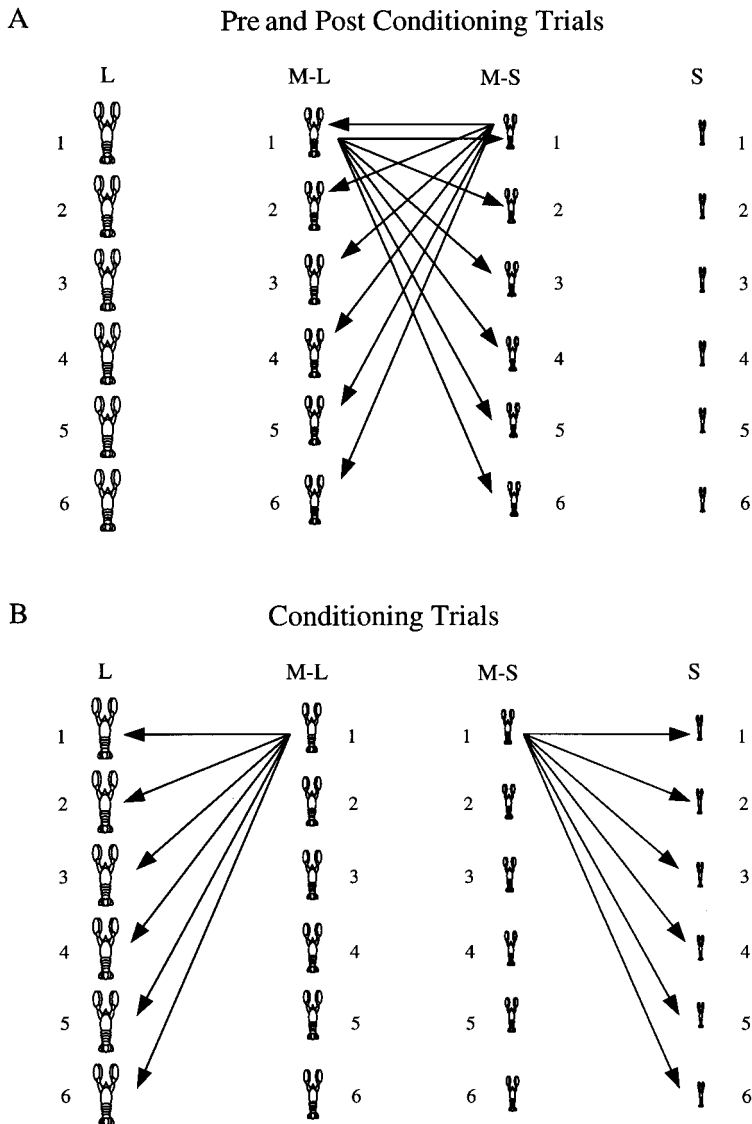


FIGURE 1 Diagram illustrating the experimental design used in the study. A. During pre and postconditioning trials each Medium-Large (M-L) crayfish fought each Medium-Small (M-S) crayfish such that all possible pairwise interactions were performed. Arrows show pairings for one individual from each group for clarity. B. During conditioning trials each Medium-Large (M-L) crayfish fought each Large (L) crayfish, and each Medium-Small (M-S) crayfish fought each Small (S) crayfish. Once again, all possible pairwise interactions were performed. Arrows show pairings for one individual from each group for clarity.

pitted against members of the L size class, and the M-S individuals ('losers') were pitted against members of the S size class. *A priori* predictions based on size differences suggested that the 'winners' would tend to lose their conditioning bouts, and the 'losers' would tend to win their conditioning bouts. As with the preconditioning fights, all possible pairwise contests were performed (Fig. 1). Each crayfish participated in two trials a day for three days.

Postconditioning Fights

After the three days of conditioning fights, individuals from the M-L ('winners') group were paired with individuals from the M-S ('losers') group. Once again, each crayfish participated in two trials a day for three days, and all possible pairwise contests were performed (Fig. 1).

Data Analysis

Differences in the performance of individuals between the pre and postconditioning fights were analyzed using a two-tailed Wilcoxon matched pairs test. The total number of wins for each individual was used for the analysis.

RESULTS

In the preconditioning trials the M-L crayfish won more of their encounters than did the M-S crayfish against which they fought (see Table I). M-L crayfish won an average of 5 fights out of the possible 6 (*SD* 1.25), while M-S crayfish won an average of 1 fight (*SD* 0.89). During the conditioning trials, however, where the M-L crayfish fought against the L crayfish, the M-L individuals only won an average of 0.17 fights (*SD* 0.41). This difference was found to be significant (two-tailed Wilcoxon matched pairs test, $T=0$, $z=2.2$, $p<0.05$). Similarly, the M-S crayfish won an average of 3.17 of the fights against the S crayfish (*SD* 1.94), which was found to be significantly different to their performance in the preconditioning trials (two-tailed Wilcoxon matched pairs test, $T=0$, $z=2.2$, $p<0.05$). During the postconditioning trials, in which the M-L crayfish once more fought the M-S crayfish, the M-L individuals won an average of 3.17

TABLE I Number of wins and losses for the Medium-Large (M-L) and Medium-Small (M-S) crayfish during the preconditioning fights (in which 6 M-L crayfish fought 6 M-S crayfish), conditioning fights (in which the 6 M-L crayfish fought 6 Large (L) crayfish and the 6 M-S crayfish fought 6 Small (S) crayfish), and postconditioning fights (in which the 6 M-L crayfish fought the 6 M-S crayfish again)

Crayfish group	Preconditioning		Conditioning		Postconditioning	
	Wins	Losses	Wins	Losses	Wins	Losses
<i>Winners</i>						
M-L1	6	0	0	6	4	2
M-L2	6	0	0	6	3	3
M-L3	6	0	1	5	4	2
M-L4	5	1	0	6	4	2
M-L5	4	2	0	6	1	5
M-L6	3	3	0	6	3	3
<i>Losers</i>						
M-S1	2	4	3 ^a	2	4	2
M-S2	2	4	6	0	4	2
M-S3	1	5	5	1	3	3
M-S4	1	5	2	4	2	4
M-S5	0	6	1	5	2	4
M-S6	0	6	2	4	2	4

^aOne bout resulted in no clear winner or loser, and so was not included in the analyses.

fights (*SD* 1.17) and the M-S individuals won an average of 2.83 fights (*SD* 0.98). In both cases these were found to be significantly different to the outcomes of the pre-conditioning trials: the M-L crayfish won significantly fewer fights than they had previously (two-tailed Wilcoxon matched pairs test, $T=0$, $z=2.2$, $p<0.05$), and the M-S crayfish won significantly more fights (two-tailed Wilcoxon matched pairs test, $T=0$, $z=2.2$, $p<0.05$). Hence the three-day conditioning period significantly altered the likelihood of winning subsequent encounters.

DISCUSSION

This study highlights the important and poorly-understood role of social experience in crustacean agonistic encounters. We show that recent wins or losses in a series of fights can alter the likelihood of an individual winning a subsequent encounter, despite an apparent disparity in size between opponents that would otherwise serve as an accurate predictor of the outcome. This is particularly noteworthy in the decapod crustaceans given the results of previous studies showing the importance of size in agonistic encounters. For example, prior residence is a form of social experience that has been shown to predict the outcome of agonistic encounters, but it was insufficient to reverse the effects of size asymmetry in bouts between female prawns (Evans and Shehadi-Moacdieh, 1988).

The results of the preconditioning trials are consistent with the bulk of the literature on crustacean aggression, which documents the importance of size in determining the outcome of agonistic interactions (Bovbjerg, 1953, 1956; Rubenstein and Hazlett, 1974; Evans and Shehadi-Moacdieh, 1988; Ranta and Lindström, 1992, 1993; Figler *et al.*, 1995a; Pavey and Fielder, 1996). These results are also consistent with game theory models in which individuals alter their decision to continue fighting, escalate, or retreat based on an assessment of possible size asymmetries (Hack, 1997; Whitehouse, 1997; Nowbahari *et al.*, 1999; Moya-Laraño and Wise, 2000). In keeping with these findings, the M-L individuals (which ranged from 2 to 97% greater in mass than the M-S individuals) won significantly more of their preconditioning fights than did their M-S opponents. Claw size is often highlighted as an important factor in determining the winner, sometimes serving as a more reliable predictor than carapace size (Barki *et al.*, 1991, 1997; Garvey and Stein, 1993; Rutherford *et al.*, 1995; Sneddon *et al.*, 1997). The results of the preconditioning trials are similarly consistent with these findings.

Nevertheless, measures of size are not the only predictors of victory in an encounter between crustaceans. The reproductive status of females has been shown to alter the likelihood of winning an aggressive encounter, with gravid females defeating males despite a size disadvantage (Figler *et al.*, 1995b; Mello *et al.*, 1999). Previous social experience has also been shown to contribute to the outcome of an agonistic interaction (Dunham, 1972; Rubenstein and Hazlett, 1974). Goessmann *et al.* (2000) recently demonstrated 'winner' and 'loser' effects in the crayfish *Astacus astacus*, whereby winning one bout increases the likelihood of an individual winning subsequent bouts and losing a bout increases the likelihood of further losses. However, such studies usually involve size-matched individuals to minimize the confounding effects introduced by size differences – a sensible precaution given that small differences in chelae dimensions, exoskeleton calcium concentrations, and plasma protein levels

can affect the outcome of a bout when opponents are otherwise closely matched in size (Vye *et al.*, 1997).

The results of the conditioning and postconditioning trials carried out in this study show that recent social experience, such as winning or losing a series of bouts, can significantly alter the likelihood of winning a subsequent encounter, even when faced with a size difference that would otherwise be sufficient to determine the outcome. In the postconditioning trials, after a series of conditioning trials in which the M-S crayfish experienced victories over smaller crayfish, the M-S crayfish fared significantly better against their M-L opponents than they had previously done in the preconditioning trials. Likewise, after the conditioning trials in which the M-L crayfish lost to larger crayfish, the M-L crayfish fared significantly less well against the M-S crayfish. Thus, the experiences of both groups during the conditioning trials were sufficient to substantially alter (though not completely reverse) the trend of outcomes seen in the preconditioning trials.

The role of social experience in determining the outcome of agonistic encounters is clearly an important one, capable in some instances of reversing trends set by physical factors such as size and chelae length. The relationship between experience and the outcome of subsequent bouts is, however, not simple. For example, some studies carried out on fish reported 'loser' effects but not 'winner' effects (Francis, 1983; Beecham and Newman, 1987), while others reported both effects (Beaugrand *et al.*, 1991; Chase *et al.*, 1994; Hsu and Wolf, 1999). Similarly, a study carried out on birds found a 'winner' effect but no 'loser' effect (Jackson, 1991).

Even when both 'winner' and 'loser' effects are discovered, they should not be assumed to have equal and opposite magnitude. In a study carried out on fish, Frey and Miller (1972) noted that losing an encounter had a substantially greater chance of altering future outcomes than did winning an encounter. Hsu and Wolf (1999), also working on fish, noted that the 'winner' and 'loser' effects seemed to follow different time-courses. Goessmann *et al.* (2000) similarly described separate time-scales for the actions of 'winner' and 'loser' effects in crayfish.

These findings are consistent with the different levels of success achieved by the conditioning trials in reversing prior status as 'winners' or 'losers'. Though the 'losers' won more of their conditioning trials than preconditioning trials, the number of reversals was not as great as seen in the 'winners'. One explanation for this is that the 'loser' effect may be more difficult to reverse than the 'winner' effect. However, an alternative explanation for the apparent difference in efficacy of the conditioning trials must also be considered. The M-S animals were more closely matched in size with their S counterparts than were the M-L animals with the L animals. This lesser size advantage, possibly further compromised in some instances where the chelae size of the M-S and S animals overlapped, may have reduced the predictive value of the size classes to which the individual crayfish were assigned. Hence the relative strength of 'winner' and 'loser' effects can not be gaged reliably from the present study.

Further complications arise when dealing with effects of social experience, such as 'winner' and 'loser' effects; care must be taken to avoid confounding issues. The study carried out by Hsu and Wolf (1999) attempted to determine whether the order of a sequence of winning and losing events altered the subsequent likelihood of winning. In doing so, however, they varied not only the order of winning and losing experiences but also the total number of wins and losses an individual may have experienced, confounding any order effect with a possible total experience

effect. In other studies, the effect of losing a bout has been shown to outweigh size asymmetries of up to 20% in pumpkinseed sunfish (Beacham, 1988), and up to 40% in green swordtail fish (Beaugrand *et al.*, 1991). However, these studies (and many others) selected their ‘winners’ and ‘losers’ by the result of their initial encounter. As pointed out by Begin *et al.* (1996), this self-selection alters the probability of subsequent wins and losses. An individual that wins its first encounter may have held some prior advantage, and so can no longer be assumed to have a 50% probability of winning any subsequent encounters. If the individual proceeds to win the next encounter there is no way to tell whether it was due to a ‘winner’ effect or simply the same advantage that allowed it to win the first encounter.

With crayfish the situation is further complicated by the ability of individuals to recognize the dominance status of their opponents via chemical cues (Zulandt *et al.*, 1999). Changes in fighting behavior may therefore result from a combination of ‘winner’ and ‘loser’ effects, and the recognition of higher or lower dominance status on the part of the combatants. In addition, each M-S individual fought each M-L individual twice – once in the preconditioning trials and once in the postconditioning trials – so individual recognition between protagonists cannot be discounted. However, if individual recognition was playing a major role in the outcome of the postconditioning trials it should have worked against the social experience provided during the conditioning trials, favoring the same results in the postconditioning trials as were observed in the preconditioning trials. Given that this was not the case, social experience may have potentially overcome not only a size asymmetry, but also individual recognition.

As a result of these considerations, the experimental design used in this study did not attempt to distinguish between ‘winner’ and ‘loser’ effects in the outcome of the post-conditioning trials. We avoided the self-selection of winners and losers by using conditioning trials to provide the necessary social experience. However, requiring the winners to fight the losers in the postconditioning trials does not allow us to determine the relative contribution of ‘winner’ and ‘loser’ effects. Hence, we limit our conclusions to the more general term social experience: we defer the examination of the relative importance of ‘winner’ and ‘loser’ effects for future studies.

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