

Communication networks and loser effects interact to influence the outcome of aggressive interactions in the crayfish *Orconectes rusticus*

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Summary

Dyadic interactions occur in the vicinity of non-participating animals such that bystanders have the potential to extract relevant information about future opponents. Individuals within communication networks can use information to modify their behaviour in future encounters with a previous fighter. Previous research on crayfish (*Orconectes rusticus*) has shown that watching fights negatively impacts the ability of bystanders to win against naïve opponents. We examined the role of visual information in communication networks and previous social history, in the form of winner and loser effects, in shaping crayfish aggression and outcomes of aggressive encounters. Experimental treatments consisted of allowing a bystander to observe a fight and then engaging that bystander with either the winner or loser in a subsequent encounter. Our results indicate that previous social history is more influential in determining fight outcome than information gathered via visual signals. Specifically, loser effects have a greater influence on fight dynamics than elements of communication networks. Since crayfish use a combination of sensory cues during social interactions, visual information may not provide the proper context for information use in subsequent interactions. We conclude that previous social history may be masking any effects that visual communication networks have on agonistic behaviour in crayfish.

Keywords: crayfish, social history, communication networks.

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Introduction

Studies on agonistic behaviour have traditionally been limited to analyses of dyadic interactions; however, recently research has started to examine agonistic behaviour within the context of the broader social environment (Johnson & Akerman, 1998; Oliveira et al., 1998; Peake et al., 2001, 2002, 2005). In the broader social environment, communication networks are established as signals travel farther than the distance between two communicating individuals and include bystanders that are within the active spaces, and previous social history of the combatants (McGregor & Peake, 2000; Peake, 2005; Bonnie & Earley, 2007). Potential factors that can alter social behaviour in a network setting include social eavesdropping (Oliveira et al., 1998; Peake et al., 2001, 2002), priming (Oliveira et al., 2001; Matos et al., 2003), and reverse priming (Earley et al., 2005; Zulantz et al., 2008). In addition to the information transfer in communication networks, social history, such as winner and loser effects, can also occur (Earley & Dugatkin, 2002). The integration of communication network theory with social history has been termed social information (Bonnie & Earley, 2007). Underlying the individual phenomenon contained within social information theory are different behavioural mechanisms which can interact to produce different consequences for signalers and receivers in a communication network or winners and losers in social history.

In communication networks, bystanders can obtain additional information that can be used in future encounters in social eavesdropping (McGregor & Peake, 2000); they can also experience physiological or behavioural called priming or reverse priming that lead to future fight success (Oliveira et al., 2001; Clotfelter & Paolino, 2003; Earley et al., 2005). Social eavesdropping allows bystanders to obtain information on the quality of potential future combatants such as fighting ability or resource holding potential (RHP; Parker, 1974; Oliveira et al., 1998; McGregor & Peake, 2000). Both priming and reverse priming likely involve a change in the neuroendocrine modulators of aggression that contribute to future fight success (Bronstein, 1989; Potegal, 1991; Oliveira et al., 2001; Matos et al., 2003; Earley et al., 2005). These modulators include hormones and neurotransmitters in fish (Oliveira et al., 1996, 2001, 2002) and in crustaceans (Huber et al., 1997; Huber & Delago, 1998; Kravitz & Huber, 2003). Although the three previous mechanisms (social eavesdropping, priming, and reverse priming) all contribute to

future fight success, social information use also includes effects from previous social history.

Previous social history, in the form of winner and loser effects, occur when an animal has an altered probability of outcomes in subsequent encounters after experiencing either a winning event or a losing event (Dugatkin, 1997; Hsu & Wolf, 1999, 2001; Dugatkin & Earley, 2003; Hsu et al., 2006). For example, individuals who experience a win increase their probability of winning future fights (Dugatkin, 1997; Hsu & Wolf, 1999; Bergman et al., 2003). The opposite is true for losers; individuals are more likely to lose future encounters (Dugatkin, 1997; Hsu & Wolf, 1999; Dugatkin & Earley, 2004). Several mechanisms contribute to the manner in which previous social history shapes future behaviour, and some of these mechanisms are shared with the elements in a communication network. These mechanisms include neuroendocrine changes (Oliveira et al., 1996; Edwards & Kravitz, 1997), learning (Karavanich & Atema, 1998; Zulantz Schneider et al., 2001) and changes in fighting skill (McDonald et al., 1968; Thines & Heuts, 1968). Winner and loser effects are documented in many taxa (Hsu et al., 2006).

Within the broader context of social information use, social history and bystander effects in communication networks (i.e., social eavesdropping, priming, and reverse priming) interact to influence future fight success (Oliveira, 2005). The interaction of social history and bystander effects can be tested using aggression in crayfish (Daws et al., 2002; Bergman et al., 2003; Zulantz et al., 2008). Previous social history contributes to the formation and maintenance of crayfish dominance hierarchies in the form of winner and loser effects (Goessmann et al., 2000; Daws et al., 2002; Bergman et al., 2003). Furthermore, preliminary work on communication networks in crayfish has shown that bystanders are negatively influenced in future fights with naïve opponents (Zulantz et al., 2008). In the field, agonistic interactions are brief and often occur within the presence of other crayfish, indicating that there is potential for crayfish to use communication networks (Bergman & Moore, 2003).

In this study, we chose to expand the scope of social information use in crayfish by examining how social history, and social eavesdropping influence the outcome of crayfish agonistic interactions. Previous research has shown that crayfish alter their behaviour after observing agonistic interactions between conspecifics (Zulantz et al., 2008). Our experimental design extends these studies allowing us to examine the relative roles that previous social

history and network elements have on regulating aggression in crayfish. By fighting bystanders against both seen and unseen winners and losers, we will be able to separate network effects from previous social history effects. We predict that if winner and loser effects are the primary factors regulating aggression, we will not observe any differences in the probability of winning and/or aggression exhibited during the contest of the focal crayfish in our control treatments (unseen winners and losers) versus our experimental treatments (seen winners and losers). However, if bystanders are obtaining and using information from the interaction, then we predict that we will see differences in the fighting ability of focal crayfish in encounters with unseen winners and losers compared to fights with seen winners and losers.

Materials and methods

Animals

Male crayfish, *Orconectes rusticus*, were collected from the Portage River near Bowling Green, OH, USA. Crayfish were housed in individual opaque containers (9.0 cm depth; 17.8 cm diameter), that served to physically and socially isolate individuals from other crayfish. These opaque containers were stored in a flow-through tank (48 × 154 × 31 cm) within an environmental chamber at a constant temperature and light/dark cycle (23°C, 12L : 12D). Intermolt form I (reproductive) male crayfish (mean ± SE, carapace 3.3 ± 0.02 cm, chelae 3.0 ± 0.03 cm, weight 12.3 ± 0.20 g) with fully intact sensory appendages had no social experience for at least 1 week prior to experimentation to remove any previous social effects on experimental outcomes (Karavanich & Atema, 1998; Zulantz Schneider et al., 2001). All crayfish were fed one rabbit pellet three times per week. Crayfish were sized-matched to within 10% of carapace and chelae length of opponents to counteract any size impacts on fight outcome.

Fight arena

The fight arena was made of clear Plexiglas (40 × 40 × 14 cm) and was filled with 10 litres of dechlorinated water (4 cm from the top of the tank, Figure 1). Two of the outer sides of the fight arena were clear, the other two opaque. The fight arena was divided into four quadrants, separated by opaque

retractable walls. Two additional small arenas were used as bystander tanks ($20 \times 10 \times 14$ cm) and were placed adjacent to the clear walls of the fight arena. Bystander tanks had three opaque walls and one clear wall so that crayfish in each trial would be within visual range of one another.

Bystander conditioning fights

This project consisted of testing four conditions with a bystander facing a winner or a loser in each condition. Each trial consisted of two elements, a bystander conditioning treatment followed by the experimental fight. The bystander conditioning fight served dual purposes in that a 'winner' and a 'loser' crayfish were determined and a bystander observed this fight. The experimental fight was used to measure any behavioural impact of observation by pairing the bystander crayfish against either the winner or loser crayfish from the conditioning fight.

During the bystander conditioning fight, a socially naïve crayfish was designated as the bystander and was placed in an adjacent bystander tank (see Figure 1). Additionally, socially naïve crayfish (hence named tester crayfish) were placed on opposite sides of the retractable wall in the fight arena (see Figure 1). All crayfish in each trial were size-matched and were allowed to acclimate for 20 min. After the acclimation period, the wall was removed and the two tester crayfish were allowed to interact for 15 min with the bystander crayfish within visual range of the interaction. Bystander crayfish did not physically interact with the tester crayfish in the initial fight. During the bystander conditioning fight, a human observer watched the encounter and determined the winner and loser of the fight between the two tester crayfish. Winners were determined when opponents (losers) retreated or tail-flipped away (Bergman et al., 2003).

Experimental fights

After the conclusion of the bystander conditioning fight, a bystander crayfish and a tester crayfish (either a winner or loser) were placed on opposite sides of an opaque wall in a separate identically-sized fight arena. During the experimental fight, both the bystander and tester crayfish were allowed to acclimate for another 20 min. The wall was then removed and the two crayfish were allowed to interact for 15 min. Bystander crayfish were exposed to one of two treatments (winner or loser) combined with one of four conditions. The four conditions were:

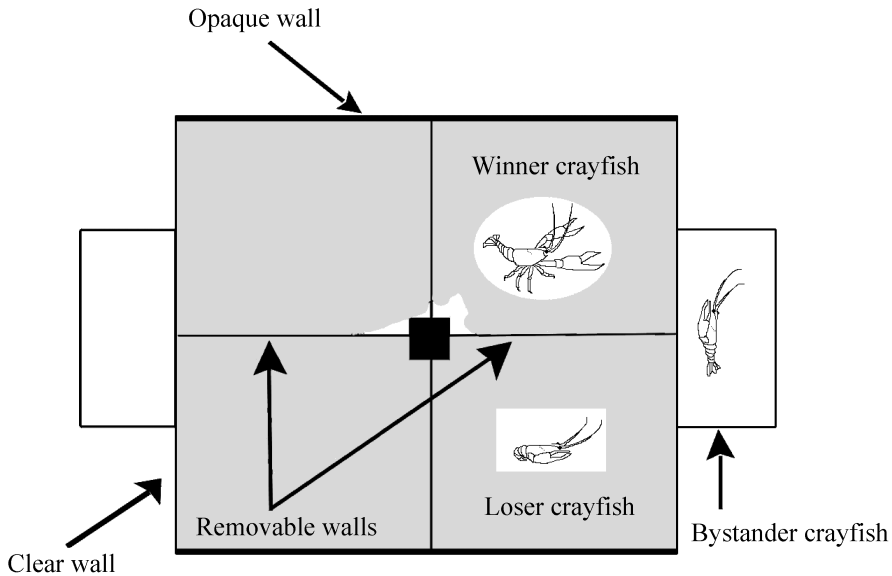


Figure 1. The observational learning arena. Two trials were run at once in this set-up. The walls next to the bystander tanks were clear allowing crayfish to be within visual range of each other. The other two walls of the fight arena were opaque. Bystander crayfish were placed in the adjacent boxes while two tester crayfish were placed on opposite sides of an opaque wall in the fight arena. The walls were removed in order to allow tester crayfish to interact.

1. 15-min agonistic encounter with the tester crayfish of the previous fight (fight condition).
2. 15-min agonistic encounter with a tester crayfish after watching two crayfish that did not interact (i.e., the wall was not removed, visual control).
3. 15-min agonistic encounter with a tester crayfish after watching an empty tank (handling control).
4. 15-min agonistic encounter with a tester crayfish after watching the wall being removed with no crayfish present (motion control).

For each of the control treatments, a separate (non-observed) conditioning encounter was performed in order to establish a winner or loser tester crayfish that would be used in the experimental fights. This separate agonistic encounter was run simultaneously as the bystander conditioning control. Each condition group consisted of 20 trials. Thus, a total of 160 bystander crayfish were used for two treatments (winner and loser) and four conditions

(fight condition, visual, handling, and motion controls). Bystander crayfish were used only once in this experiment.

Data analysis

All fights were recorded from a camera (Panasonic wv-CL350) positioned one meter above the test arena, displayed on a monitor (Sony PVM-1351G), and recorded to a VCR (Panasonic AG-1980). Agonistic encounters were recorded for subsequent analysis. A blind analysis was performed by a person with no prior knowledge of which treatment or condition each crayfish was assigned to for the experimental fight. For each agonistic encounter, the winner and loser of each fight was recorded. Also, the temporal mechanics of the fight were recorded (see Table 1 for descriptions), which included time to different fight intensities and duration of the initial encounter. We used a modified ethogram to determine time to different intensities (Bergman et al., 2003; Table 1). To analyze data within each treatment (for bystander effects), initiation and winning were analyzed using a modified chi-square analysis ($\chi^2 = 7.82$, $df = 3$), followed by a contingency table for multiple proportions ($q_{0.05, \infty, 4} = 3.63$), similar to a Tukey post-hoc analysis (Zar, 1999). The temporal mechanics of the fight were analyzed using a one-way MANOVA, followed by a Tukey post-hoc test, if needed. We also performed analyses across the winner and loser treatments (to test for social history effects) using a chi-square analysis ($\chi^2 = 14.07$, $df = 7$) followed by a contingency table for multiple proportions ($q_{0.05, \infty, 8} = 4.29$, Zar, 1999). A 2×4 factorial MANOVA, with type of treatment (winner or loser) and bystander condition (fight, visual control, handling control, or motion control), followed by a Tukey post-hoc was used to analyze fight dynamics. Furthermore, a *G*-test

Table 1. Crayfish ethogram codes (fight intensity levels).

Intensity level	Behaviour
-2	Tail-flip away from opponent or a fast retreat
-1	Retreat: slowly back away from opponent
0	No response or threat display
1	Approach without a threat display
2	Approach with threat display: antennal whip, meral spread, or raised posture
3	Initial claw use: boxing, pushing, or touching with closed claws
4	Active claw use: grab opponent with claws or hold other crayfish with claw

(with a null hypothesis of 0.67) was performed in order to test for significant winner or loser effects (Hsu et al., 2006). In addition, the percent of fights reaching intensity level 4 across the winner and loser treatments was analyzed using a chi-square analysis ($\chi^2 = 14.07$, $df = 7$) followed by a contingency table for multiple proportions ($q_{0.05, \infty, 8} = 4.29$, Zar, 1999). Significance was set at $p < 0.05$ and all data were analyzed using Microsoft Excel and Statsoft Statistica version 6.0.

Results

Initiation and winning

For winning probabilities, significant differences were found across the winner and loser treatments (Figure 2). Bystanders that had fought a winner lost significantly more fights than bystanders that fought losers ($\chi^2 = 49.96$, $p < 0.05$; Figure 2). All of the fights in the winner conditioning

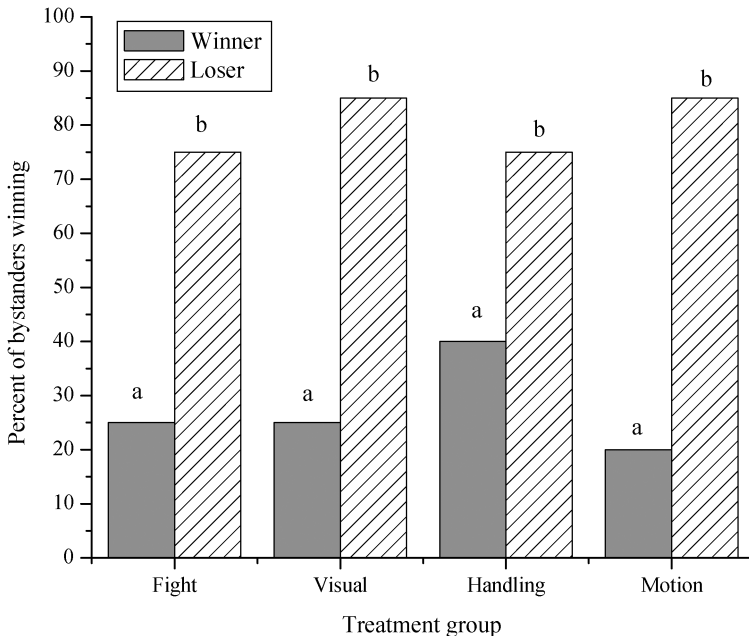


Figure 2. Percent of fights won by bystanders. Darkened bars represent the results of the bystander engaged with winners and the hatched bars are results from the loser treatment. Columns with different letters indicate significant differences using a chi-square test followed by a contingency table ($\chi^2 = 49.96$, $N = 20$, $df = 7$, $p < 0.05$).

Table 2. Critical values from the Tukey post-hoc analysis for winning probabilities between the winner and loser treatments.

Winner	Loser			
	Fight	Visual control	Handling control	Motion control
Fight	9.00	11.13	9.00	11.13
Visual control	9.00	11.13	9.00	11.13
Handling control	6.24	8.36	6.24	8.36
Motion control	10.02	12.14	10.02	12.14

All fights in the winner treatment were statistically different from fights in the loser treatment ($q > 4.29$, $p < 0.05$).

groups were statistically different from the fights in the loser conditioning groups (Table 2). We found no significant differences in winning between conditions in the winner treatment ($\chi^2 = 2.26$, $p > 0.05$; Figure 2). Within the loser treatment, there were also no statistical differences between conditions ($\chi^2 = 1.25$, $p > 0.05$; Figure 2).

Within the winner treatment, all condition proportions were statistically similar; they are homogeneous ($G_h = 2.18$; $df = 3$, $p > 0.05$). When we pooled the data for the number of times that winners won their fights, the data was not statistically different from a null proportion of 0.67 ($G_p = 1.13$, $df = 1$, $p > 0.05$). For losers who lost their fights, all condition proportions were statistically similar as well ($G_h = 1.26$, $df = 3$, $p > 0.05$). When the data were pooled, results were significantly different from the 0.67 null probability ($G_p = 6.67$, $df = 1$, $p < 0.05$).

For initiation within the winner treatment, there were no significant differences among conditions ($\chi^2 = 3.81$, $p > 0.05$; Figure 3). In the loser treatment, there was no overall significant difference between conditions ($\chi^2 = 1.80$, $p > 0.05$; Figure 3). When we compared across the winner treatment and the loser treatment, we found no significant differences in initiation ($\chi^2 = 5.10$, $p > 0.05$; Figure 3).

Fight dynamics

The percent of fights that reached fight intensity level 4 (see Table 1 for descriptions) was significantly different across the winner and loser treatments (Figure 4; Table 3). Within the winner treatment, the fight condition reached intensity 4 85% of the time, the visual control 70%, the handling

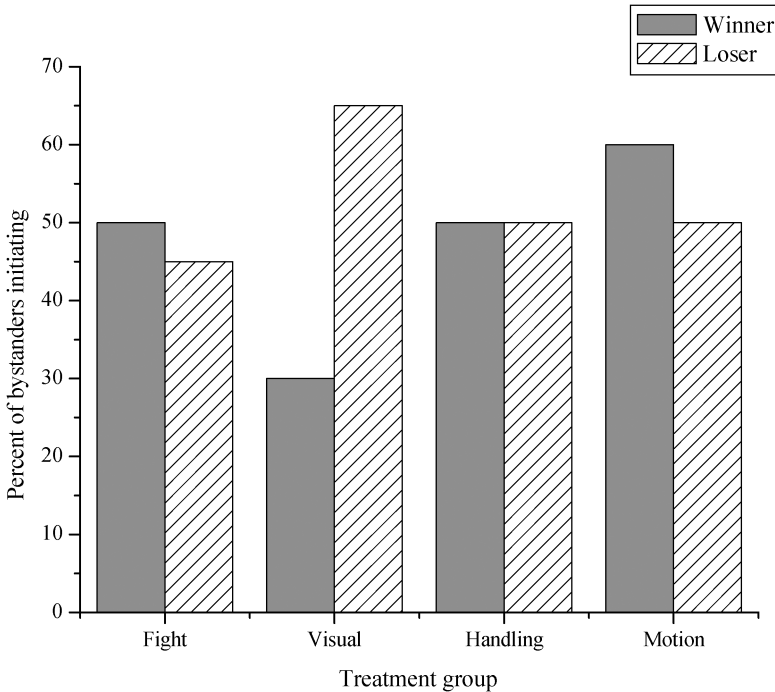


Figure 3. Percent of bystanders initiating the fight. Darkened bars represent the results of the bystander engaged with winners and the hatched bars are results from the loser treatment. Results were not statistically different and data were analyzed using a chi-square test ($\chi^2 = 5.10$, $N = 20$, $df = 7$, $p > 0.05$).

control 55% and the motion control 70%. In the loser treatment, the fight condition reached intensity 4 40% of the time; and the visual control, handling control, and motion control all reached intensity 4 45% of the time ($\chi^2 = 15.06$, $p < 0.05$; Figure 4; Table 3).

When we examined the results from the conditions, we did not find any significant differences in time to different intensities or duration in the winner treatment. In the loser treatment, there were no significant differences in time to different intensities or duration. Across the winner and loser treatments, data was not statistically different in times to different intensities (Figure 5) or in duration (Figure 6).

Discussion

We did not observe any differences in the fighting ability or fight outcome of bystanders in our control conditions (unseen winners and losers) versus our

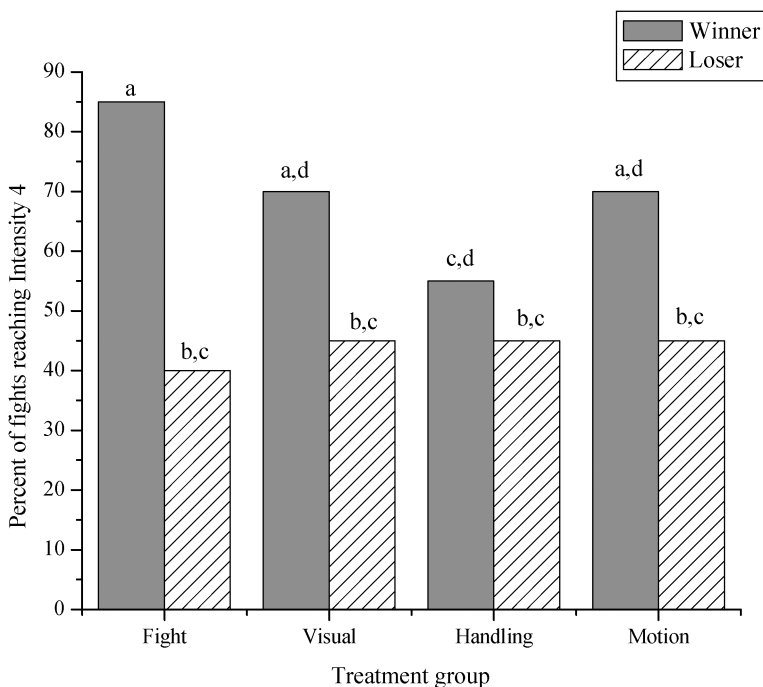


Figure 4. The percent of fights that reached intensity level 4 (Table 1). Darkened bars represent the results of the bystander engaged with winners and the hatched bars are results from the loser treatment. Columns with different letters indicate significant differences using a chi-square followed by a contingency table ($\chi^2 = 15.06, N = 20, df = 7, p < 0.05$).

Table 3. Critical values from the Tukey post-hoc analysis for the number of fights that reached fight intensity level 4 between the winner and loser treatments.

Winner	Loser			
	Fight	Visual control	Handling control	Motion control
Fight	5.28	7.49	7.49	7.49
Visual control	5.28	4.41	4.41	4.41
Motion control	5.28	4.41	4.41	4.41

All fights in the winner treatment, except the handling control, were statistically different from fights in the loser treatment ($q > 4.29, p < 0.05$).

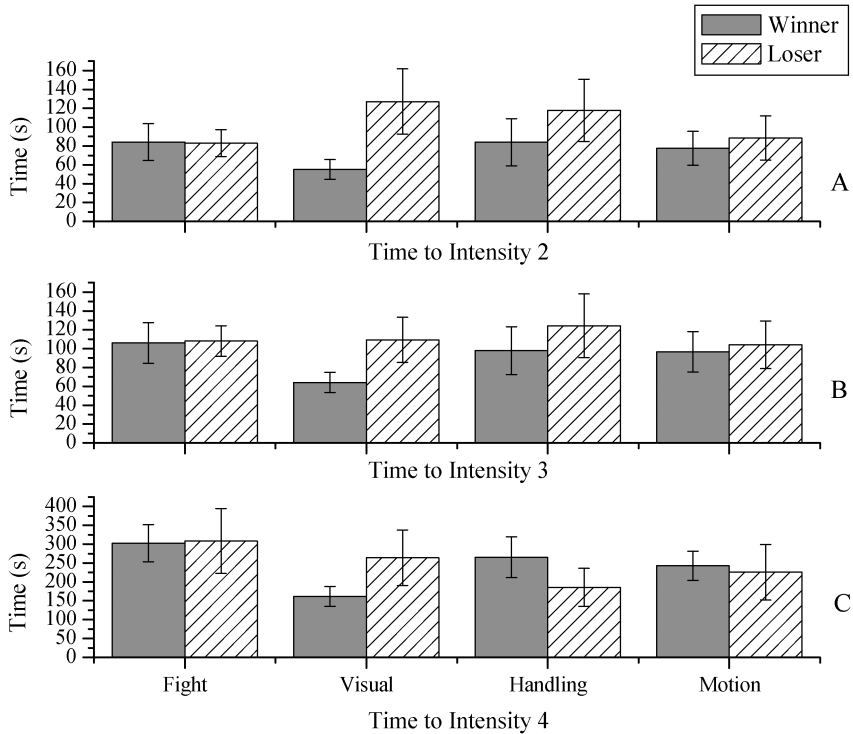


Figure 5. Time to fight intensity levels. Darkened bars represent the results of the bystander engaged with winners and the hatched bars are results from the loser treatment. Data were analyzed using a two-way MANOVA and was not statistically different for time to intensity 2 (A) ($F = 0.923$, $N = 20$, $p > 0.05$), intensity 3 (B) ($F = 0.364$, $N = 20$, $p > 0.05$) or intensity 4 (C) ($F = 0.918$, $N = 20$, $p > 0.05$).

experimental conditions (seen winners and losers). Bystander crayfish were equally as likely to win their next encounter as crayfish that had watched various control conditions in either the winner treatment or the loser treatment (Figure 2). Upon examining the results from the G -tests for the winner and loser treatments to test for significant winner or loser effects, results were not significantly different from the expected proportion of 0.67 in the winner treatment. However, in the loser treatment, the pooled results were statistically different from the 0.67 proportion, indicating that significant loser effects occurred in these experiments. Therefore, it appears that previous social history, in the form of loser effects, was more influential in determining fight outcome. We also found a trend in the maximum intensity of fights observed between the winner and loser treatments. Fight intensity 4 was the

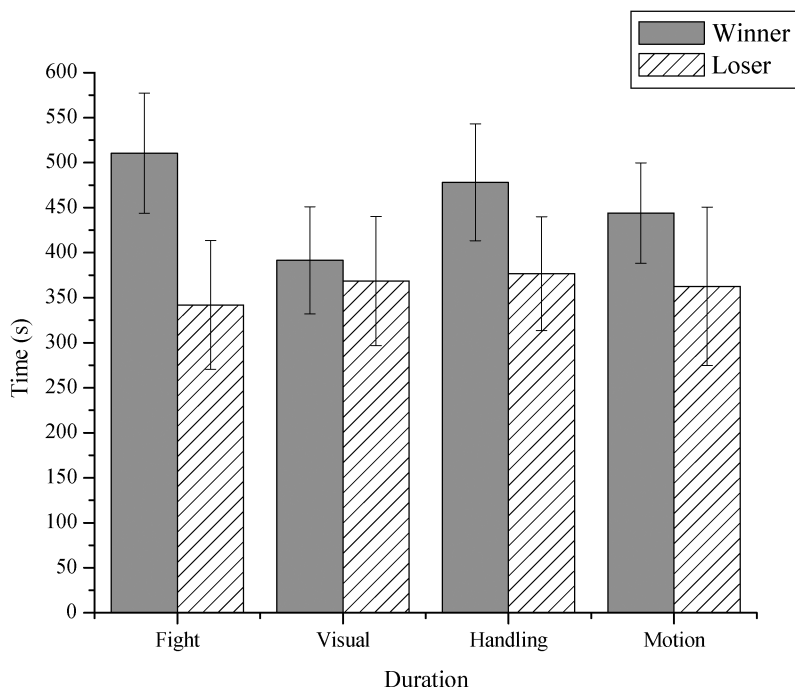


Figure 6. Duration of the experimental fight. Darkened bars represent the results of the bystander engaged with winners and the hatched bars are results from the loser treatment. Data were not significantly different and were analyzed using a two-way MANOVA ($F = 0.388$, $N = 20$, $p > 0.05$).

most intensive fight level analyzed, and all conditions in the winner treatment, except the handling control, reached intensity 4 significantly more of the time than conditions in the loser treatment (Figure 4). Therefore, fights within the winner treatment were more aggressive than fights in the loser treatment in that fights within the loser treatment reached intensity 4 only 40–45% of the time compared to 55–85% for fights in the winner treatment (Figure 4). In summary, loser effects were a larger determinant of fight outcome than bystander effects and fights within the winner treatment were more aggressive than fights in the loser treatment (Figures 2 and 4).

Within crayfish, the effects of previous social history on agonistic behaviours have been documented (i.e., Daws et al., 2002; Bergman et al., 2003). Crayfish given winning experiences are more likely to win in future encounters and losers will continue to lose in future encounters (Chase et al., 1994; Dugatkin, 1997; Hsu & Wolf, 1999; Hsu & Wolf, 2001). In this study, winner

effects did not occur, but loser effects were prominent (Figure 2). Although previous winners won against bystanders, analyzing fight outcome with a *G*-test for homogeneity allows differentiation between intrinsic fighting ability and winner effects. Since our results in the winner condition did not differ significantly from a 0.67 proportion, fight outcome was more likely due to intrinsic fighting ability over winner effects. Previous losers lost against bystanders greater than 67% of the time; indicating that the loser effect exists in crayfish (Figure 2). Mechanistic studies have strongly indicated that the behavioural effect is most likely connected to changes in the underlying neurochemistry. For instance, changes in neurochemistry in killfish (*Kryptolebias marmoratus*), did not directly predict future fight success (Earley & Hsu, 2008). Rather, a complex reciprocity was demonstrated in agonistic interactions in that changes in hormone levels were resultant from fight dynamics rather than fight outcomes (Earley & Hsu, 2008). While differences in the neurochemistry of winners and losers can influence their ability to win or lose future encounters, there is not a direct causal relationship between hormone levels and contest outcome. In addition, priming effects are mediated by changes in neurochemistry (Yeh et al., 1997; Oliveira et al., 2001; Earley et al., 2005). Although winner and loser effects are inherently different from priming and reverse priming, both can be modulated by neurochemistry or changes in neuroendocrine mechanisms.

Reverse priming is a down regulation, or up-regulation of the physiological mechanisms responsible for mediating social behaviour (Earley et al., 2005; Zulantz et al., 2008). The result is that individuals are less aggressive and are more likely to lose in future fights due to changes in neurochemistry (Earley et al., 2005; Zulantz et al., 2008). In a previous study on crayfish, bystanders were more likely to lose fights against naïve males after watching a previous encounter (Zulantz et al., 2008). The authors hypothesized that reverse priming was contributing to fight outcome. By taking the previous study into account, we theorize that reverse priming contributes to our results significantly in the winner treatment, but loser effects are masking any reverse priming effects seen in the loser treatment.

It is possible that both previous social history effects and reverse priming effects are operating through the common mechanism of modulation of the physiological basis of aggression. Zulantz et al. (2008) hypothesized that crayfish exhibited reverse priming after watching fights. The effects of reverse priming can be due to changes in neurochemistry that may or may

not change future behaviour (Earley et al., 2005). In addition, winner and loser effects can also be mediated by changes in neurochemistry (Hsu et al., 2006). Of the neurotransmitters, serotonin has received the most attention in crustacean systems (Edwards & Kravitz, 1997; Huber et al., 1997). The function of serotonin is opposite in invertebrates compared to vertebrates in that having increased levels of serotonin is usually found in conjunction with heightened levels of aggressiveness (Edwards & Kravitz, 1997). The pathways of serotonin are different in dominant versus subordinate animals and can, thus, be modified by social history (Yeh et al., 1997). In addition, reverse priming could be interacting with the function of serotonin and contributing to fight dynamics. In the winner conditions, the effects of reverse priming may be contributing significantly to fight outcome while in the loser conditions, loser effects were strong enough to mask any effects of reverse priming (Figure 2). In conclusion, it is possible that the common neural mechanism of both social history and reserve priming is either masking or overriding any effects that visual communication networks have on modifying crayfish aggression in the loser conditions and driving fight outcome in the winner conditions.

In addition, it appears that we can exclude priming, from having influenced our results. In priming, fighters experience changes in levels of hormones and neurotransmitters and are more aggressive in the initial stages of fighting, fights reach higher intensity levels, and combatants are more likely to win future encounters (Bronstein, 1989; Potegal, 1991; Oliveira et al., 2001). If crayfish exhibited priming, we would predict that bystander crayfish would either have more initiations or win against both seen winners and losers more than their respective controls. As our results indicate, we did not observe these behavioural parameters and, therefore, we conclude priming did not occur in these experiments.

The final effect of communication networks that may have contributed to our results was visual social eavesdropping. If visual eavesdropping were to influence crayfish fights, we would expect that bystanders would either behave differently towards seen vs. unseen winners and losers or have different outcomes of the aggressive interactions. However, we cannot exclude visual eavesdropping due to the experimental set-up. Our set-up allowed bystanders to view agonistic interactions across a clear barrier, which in turn allows the fighters to view the bystander. It is possible that the bystander interacted visually with the fighters before the bystander vs. winner or the bystander

vs loser fight. However, our results show no differences in initiation, winning, or fight dynamics within conditions for the winner and loser treatments. Furthermore, in the winner treatment, fights were more aggressive, indicating that familiarity is unimportant. The prediction would be that familiarity would produce less intense fights. Therefore, we believe that visual eavesdropping is either not occurring in these experiments or the effects of visual eavesdropping are being masked by the effects of previous social history.

This study has shown that fight outcome is more heavily influenced by previous social history than by visual communication networks. This result could arise from a common mechanism of neurochemistry underlying reverse priming and social history (Yeh et al., 1997). Additional work is needed on the functioning of hormones, biogenic amines, and other physiological modulators in communication networks.

Social information use has been proposed as a broader framework that includes social experience and communication networks (Bonnie & Earley, 2007). Even though we did not observe any effect of visual social eavesdropping, which is in contrast to previous studies on fish, crayfish bystanders may require multiple sensory cues, including chemical cues, for social eavesdropping to have any effect. Chemical communication is important during crayfish agonistic encounters as status recognition of opponents is conveyed most likely through urine release (Breithaupt & Eger, 2002; Bergman et al., 2005). Although bystanders could not communicate chemically with opponents during the initial fight, they could during the second fight. Bystanders likely detected the social status of their opponent during the second fight and responded accordingly depending on if the opponent was a previous winner or a loser. Studies have shown that when the ability to detect chemical signals has been removed, winner effects were eliminated, indicating that crayfish require chemical information in order to identify the social status of opponents (Bergman et al., 2003). Crayfish are nocturnal, and are found in a wide variety of habitats including turbid environments, which can limit visual communication between opponents. Therefore, bystanders may need both types of information (visual and chemical) in order for any social eavesdropping to be observed. Future studies are needed on chemical communication networks and the role that social history plays in those.

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