



Observing agonistic interactions alters subsequent fighting dynamics in the crayfish, *Orconectes rusticus*

THOMAS ZULANDT*†, REBECCA A. ZULANDT-SCHNEIDER*† & PAUL A. MOORE*†

*Laboratory for Sensory Ecology, Department of Biological Sciences, Bowling Green State University
†J. P. Scott Center for Neuroscience, Mind & Behaviour, Departments of Biological Sciences and Psychology, Bowling Green State University

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In many species, social interactions play a key role in deciding resource allocation. Aggression is one mechanism by which crayfish become dominant, which, in turn, enables them to acquire higher-quality resources. In crayfish, hierarchies and dominance structures are formed by dyadic interactions. In natural habitats, crayfish have agonistic interactions that often take place with other crayfish in the vicinity. There is a possibility for observers to gain information about potential future opponents. We were interested in examining the impact of observing agonistic interactions on the social behaviour of a bystander crayfish. Bystanders were visually exposed to one of four treatments followed by an agonistic interaction with a naïve individual. Treatments consisted of: (1) two size-matched crayfish fighting (fight treatment); (2) two size-matched crayfish not fighting (visual control); (3) an empty fight arena with a retractable wall (motion control); or (4) an empty tank with no retractable wall (handling control). The second interaction, where the bystander crayfish was fought against a naïve size-matched individual, or tester crayfish, was analysed by a person, blind to treatment, for initiation, winner–loser and temporal dynamics of escalation. Our results indicate that bystander crayfish exposed to the fight treatment lost significantly more often to tester crayfish than bystander crayfish subjected to control treatments. In addition, there were changes in the fight dynamics for the bystander crayfish. These results show that observations of interactions by a third crayfish have implications for hierarchies and social behaviour in natural settings.

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Recently, a number of studies have focused on the impact that prior behavioural events can have on subsequent fighting behaviour (McGregor et al. 2000; Oliveira et al. 2001; Earley & Dugatkin 2002; Hsu et al. 2006). In particular, these studies have focused on the influence that observing fights between paired conspecifics has on the subsequent aggressive state or final dominance status of the observing animal (Earley & Dugatkin 2002; Clotfelter & Paolino 2003). Watching agonistic interactions can result in increased aggression (Oliveira et al. 2001; Clotfelter & Paolino 2003) or no change in the observing animal (Earley et al. 2005). These behavioural effects have been

labelled as eavesdropping (Naguib et al. 1999; Peake 2005), priming (Clotfelter & Paolino 2003), reverse priming (Earley et al. 2005) or conditioning, where the specific label depends upon the behavioural change observed and the proposed underlying neural or behavioural mechanism. Priming and conditioning are proposed to have a neuromodulatory basis (Hsu et al. 2006), whereas eavesdropping is linked to communication and information networks (Peake 2005).

In eavesdropping, there is the assumption that a third individual (henceforth termed bystander) gathers information about the aggression levels or fighting abilities of the individuals involved in an observed fight (McGregor & Peake 2000; Peake et al. 2005). In subsequent interactions, the bystander's behaviour is influenced by the information gathered about the fighting abilities of future opponents. Most of this work has been carried out with

Correspondence: P. Moore, Laboratory for Sensory Ecology, Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403, U.S.A. (email: pmoore@bgsu.edu).

vertebrate systems (birds and teleost fish) in which the bystander changes its behaviour as a result of being in the visual or auditory presence of agonistic interactions (Earley et al. 2005; Peake et al. 2005). The important aspect about the application of this interpretation is that the bystander engages either the winner or loser of the observed interaction. Within this paradigm, the bystander enters the subsequent interaction with knowledge of the resource holding potential of its opponent. The underlying mechanism governing changes in the fight dynamics is the information gained through communication pathways.

Priming occurs when the bystander experiences a change in the physiological state, which then can modulate aggression. Modulators can be either neurotransmitters, as in serotonin in crayfish (Edwards & Kravitz 1997), or circulating androgen and testosterone levels seen in fish (Oliveira et al. 2001, 2002). As a result of the observations, circulating hormone levels increase in the bystander and the increased hormonal levels result in an increase in the success rates and aggression in subsequent interactions (Clotfelter & Paolino 2003). Conversely, stress might decrease aggression and motivation in the bystander, which could lead to a drop in success in the subsequent interactions. This contrary result has been termed 'reverse priming' (Earley et al. 2005). With 'reverse priming', neurotransmitters or hormonal modulators reduce the level of aggressiveness in the bystander. Similar to priming, it is thought that reverse priming has a physiological basis. In addition, it is important to note that a reduction in the level of aggression can be achieved through either an increase (such as stress hormones) or a decrease (such as androgen) in the action of a modulator (Hsu et al. 2006).

Numerous studies have evaluated the influence of social conditioning on subsequent agonistic contests (for a review, see Hsu et al. 2006). In these instances, previous winners of social contests have a higher than random possibility of winning subsequent encounters (Hsu & Wolf 1999; Daws et al. 2002). These conditioning effects have been termed 'winner effects'. Conversely, losing a previous social encounter often leads to a decreased probability of winning the next encounter (Hsu et al. 2006), which has been called 'loser effects'. The underlying mechanism for these effects depends upon the organism of study and includes effects such as physiological changes in the neurotransmitter (Edwards & Kravitz 1997) and neuroendocrine modulation (Oliveira et al. 1996, 2002), increased information about the subsequent opponents (Peake et al. 2001, 2002) and changes in fighting skills (e.g. McDonald et al. 1968; Thines & Heuts 1968).

While many of the previous studies have shown the impact of observing interactions on the subsequent social behaviour in vertebrates, little work has been done on invertebrates. There is a wealth of knowledge of factors that influence agonistic interactions in crayfish and more recent work showing that agonistic interactions often take place in the presence of at least one if not multiple bystanders in the field (Bergman & Moore 2003). This produces a situation in which a system of communication networks, where crayfish receive prior information about

the aggressive levels or fighting abilities of potential opponents, is possible. The goal of this study was to determine whether observing a social interaction can alter the outcome of agonistic interactions. These results, combined with agonistic studies in the field (Bergman & Moore 2003) as well as knowledge of the underlying neural mechanisms (Huber et al. 1997; Huber & Delago 1998), provide an opportunity to understand this phenomenon from both a proximate and ultimate perspective. To perform these experiments we fought crayfish that observed social interactions (and various control treatments) against previously unknown naïve individuals. Both winner and loser effects are present within the crayfish agonistic system (Daws et al. 2002; Bergman et al. 2003); thus we chose to fight observing animals against naïve individuals to eliminate the confounding influence of winner and loser effects. Chemical signals play a central role in determining the dynamics and outcome of social interactions in the laboratory (Zulandt-Schneider et al. 2001), but it is unclear whether the hydrodynamics of natural habitats allows for the successful use of chemical signals during social interactions in nature (Bergman et al. 2006). Thus, we chose to focus initially on visual cues in this study. The overall objective of these experiments was to decipher the role of observing an agonistic encounter on the possible formation of dominance hierarchies and its impact on subsequent social interactions. Based on numerous vertebrate studies, we predicted that crayfish placed within the visual presence of a fight would have increased levels of aggression and would consequently win a larger proportion of interactions. These predictions are based on the concept that observing interactions will prime (through neuro or hormonal modulators) the crayfish for heightened aggression.

Crayfish are an accepted model system for aggression research (Dingle 1983; Hyatt 1983), particularly because of their ritualized fighting behaviour (Bovbjerg 1953; Huber & Kravitz 1995) and the development of a dominance hierarchy (Bovbjerg 1953, 1956; Zulandt-Schneider et al. 2001; Bergman et al. 2003; Gherardi & Pieraccini 2004). In crayfish populations, the formation of dominance hierarchies is developed through dyadic social interactions (Bovbjerg 1953; Capelli & Munjal 1982; Rutherford et al. 1995; Zulandt-Schneider et al. 2001; Daws et al. 2002; Bergman et al. 2003), where winners obtain access to food, shelter and mates (Wilson 1975; Dingle 1983; Söderbäck 1991; Hill & Lodge 1994; Rutherford et al. 1995; Edsman & Jonsson 1996; Pavey & Fielder 1996; Guiasu & Dunham 1997). This ability to secure resources results from the establishment of a dominant relationship, where it is thought that the dominant individual will have substantial growth and reproductive success due to its winnings (Berrill & Arsenaault 1984; Hill & Lodge 1994, 1999). Recent observations have shown that these encounters for resources in the field are often brief, take place in defined home ranges and occur in the presence of other crayfish (Bergman & Moore 2003). In natural populations, individuals may gain some knowledge of the relative dominance status by observing agonistic interactions between other individuals (Bergman & Moore 2003).

METHODS

Animals

All crayfish were fully intact, intermoult, form I (reproductive) male crayfish of the species *Orconectes rusticus*. The crayfish were collected from the Portage River in Wood County, Ohio, U.S.A. during the months of July, August and September. Each crayfish was visually and mechanically isolated in individual, ventilated, opaque plastic containers (17.8 cm in diameter, 9.0 cm in depth). The containers were placed in an aerated flow-through tank (48 × 154 × 31 cm) at constant room temperature (20 ± 2°C) on a 14:10 h light:dark cycle within an environmental chamber. Crayfish were isolated for a minimum of 1 week prior to experimental conditioning to eliminate any effects from previous social interactions (Karavanich & Atema 1998; Guiasu & Dunham 1999; Zulandt-Schneider et al. 2001). The diet consisted of one rabbit food pellet three times per week. Each crayfish (treatment and controls) was measured with respect to mass (26.2 ± 2.3 g), carapace length (4.1 ± 0.2 cm; designated from the tip of the rostrum to the posterior of the cephalothorax) and chelae length (0.52 ± 0.08 cm). All opponents were size-matched to within 10% of the carapace and chelae length. These measures were chosen because differences greater than 30% in these measures ensure that the larger crayfish wins the encounter (Pavey & Fielder 1996).

Fight Trial Set-up

The fight arena (Fig. 1) was constructed of clear Plexiglas (40 × 40 × 14 cm) and held 10 litres of de-chlorinated water (4 cm from the top of the arena). The arena was divided into four quadrants (20 × 20 × 14 cm), which were divided by an opaque retractable wall that matched the surrounding area in colour (Fig. 1). Finally, an additional

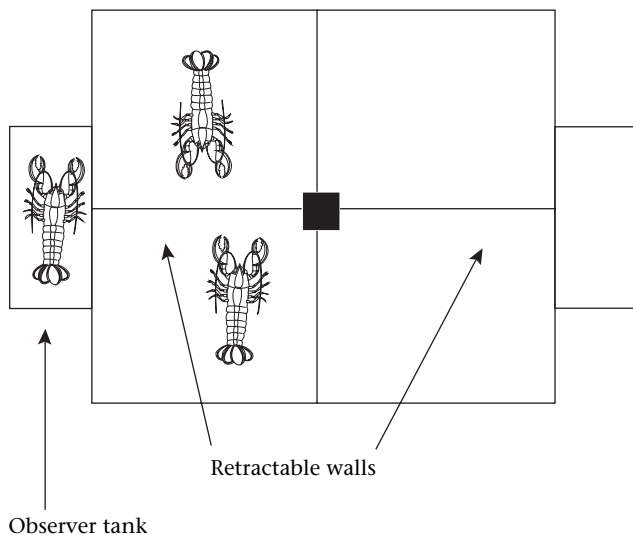


Figure 1. Fight arena showing opaque walls in place. Watcher tanks were placed on the sides where the crayfish in that tank watched two crayfish fight in the adjacent area in the fight tank.

small Plexiglas arena (observational tank: 20 × 10 × 14 cm) was located outside the fight arena. One side of the observational tank and fight arena was clear so that crayfish could be within the visual presence of each other. The crayfish engaged in the fight could also observe the bystander.

Observational Treatments

Socially naïve crayfish were placed in the observational tank with three of the walls painted black. These crayfish are referred to as the 'bystander crayfish'. This arena was then placed midway along the side of an unpainted fight arena (Fig. 1) with the clear wall facing the fight arena. Two different socially naïve crayfish were placed on either side of the removable wall in the fight arena and all three crayfish were allowed to acclimate to these conditions for 20 min. During this acclimation period, all three crayfish were visually isolated from each other. The bystander crayfish were exposed to one of four conditions:

1. a 15-min agonistic encounter between the two size-matched naïve individuals (fight treatment);
2. a 15-min period where nothing was placed in the fight tank (handling control);
3. a 15-min period where size-matched naïve individuals were placed in the fight arena but the removable wall was not pulled (visual control);
4. a 15-min period where only the fight wall was removed and no other crayfish were present (motion control).

A total of 20 bystander crayfish was used in each condition and the bystander crayfish were used only once during the experiment. Thus, a total of 80 bystander crayfish was used in the entire experiment. All observed fights reached a definitive winner or loser conclusion within the 15-min period.

Immediately following one of the four treatments, bystander crayfish were placed in a separate, yet identically sized, fight arena with a size-matched naïve opponent. This naïve opponent will be hereafter referred to as the tester crayfish. The tester crayfish was placed on the other side of the removable wall. Both the bystander and tester crayfish were allowed to acclimate in the tank for 20 min. After 20 min, the wall was removed and they were allowed to interact for 15 min.

Fight Analysis

All fights between the bystander and tester crayfish were recorded using a digital video camera (Panasonic CL350), positioned approximately 1 m above the fight arena, and a video-cassette recorder (Panasonic AG-1970). All fights were projected onto a monitor (Sony 1351 G). All trials were analysed by an observer who had no prior knowledge of the experimental status of the crayfish being analysed. A modified ethogram test, based on that of Bruski & Dunham (1987) and modified by the Laboratory for Sensory Ecology (2003, Bowling Green State University, Bowling Green, OH, U.S.A.), was used to determine different intensity levels of the bystander crayfish during fights (Table 1).

Table 1. Crayfish ethogram codes for analysing fight intensities (modified from Bruski & Dunham 1987)

-2	Tail-flip away from opponent or fast retreat
-1	Retreat by slowly backing away from opponent
0	Visually ignore opponent with no response or threat display
1	Approach without a threat display
2	Approach with meral spread threat display usually accompanied by an antennal whip
3	Initial claw use by boxing, pushing and/or touching with closed claws
4	Active claw use by grabbing and/or holding opponent with claws
5	Unrestrained fighting by pulling at opponent's claws or body parts

We recorded all levels of intensities, but negative intensities along with intensity 1 and 5 were not statistically analysed because they were so rare that we removed them from the subsequent analysis. Temporal dynamics, including latency to different intensities and the duration of the total encounter, were recorded and analysed. The duration of the encounter was measured from the start of the first interaction until a winner or loser was determined. Furthermore, the crayfish that initiated or won the fight by making the opposing crayfish tail-flip away or retreat was also recorded. These definitions of social interactions, approach and success have been published elsewhere (Bruski & Dunham 1987; Huber & Delago 1998). Statistical analysis of initiation and winning was carried out by first using a modified chi-square analysis for comparing proportions (Zar 1999). Post hoc analysis determined where, if any, statistical differences occurred and was performed using a contingency test for multiple comparison ($q_{0.05, \infty, 4} = 3.63$). Significant results are shown by $P < 0.05$ and $q_{0.05, \infty, 4} > 3.63$ (Zar 1999). The analysis for latency to different intensities and duration of the fight was performed by using a one-way MANOVA with a Fisher-LSD post hoc test.

RESULTS

Winning and Initiation Effects

The bystander crayfish that were in the visual presence of another fight (fight treatment) won significantly fewer fights against tester crayfish opponents than all other conditions: watching size-matched crayfish not fight (visual control), watching an empty tank with a retractable wall (handling control) or watching an empty tank with no retractable wall (motion control; $q = 3.75$, $q = 3.75$, $q = 3.65$, $P < 0.05$, respectively; Fig. 2). The three other treatments were not significantly different from each other ($P > 0.05$ in all other conditions).

Bystander crayfish, exposed to a fight condition, initiated significantly fewer fights against naïve opponents than bystander crayfish in visual and motion control conditions ($q = 3.93$ and $q = 4.4$, $P < 0.05$, respectively). There was no significant difference in initiating fights when comparing bystander crayfish in the fight condition to bystander crayfish in the handling condition ($q = 0.86$, $P > 0.05$; Fig. 2). In addition, there were no significant

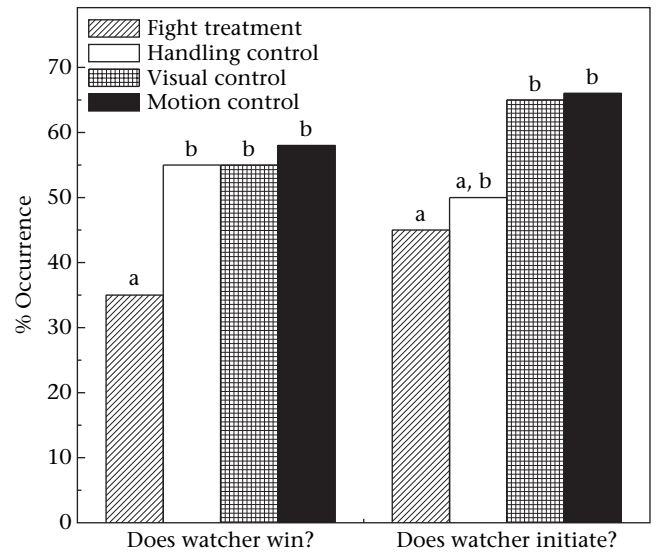


Figure 2. Percentage of watcher crayfish that initiated or won their fight with a naïve, size-matched crayfish. Treatments that do not share letters (a, b) were significantly different, while treatments that share letters were not significantly different ($N = 20$, $q_{0.05, \infty, 4} > 3.20$, $P < 0.05$).

differences between the initiations of fights with the crayfish in all the other treatments ($P > 0.05$).

Effects of Observation Treatment on Fight Dynamics

Analysis of the temporal aspects of fight dynamics also showed significant differences between the fight treatment and the other conditions. The duration of fights for the bystander crayfish under the fight treatment was significantly longer when compared to the handling, visual and motion controls ($P = 0.034$, $P = 0.018$, $P = 0.023$, $P < 0.05$, one-way MANOVA, respectively; Fig. 3). There were no significant differences found when the

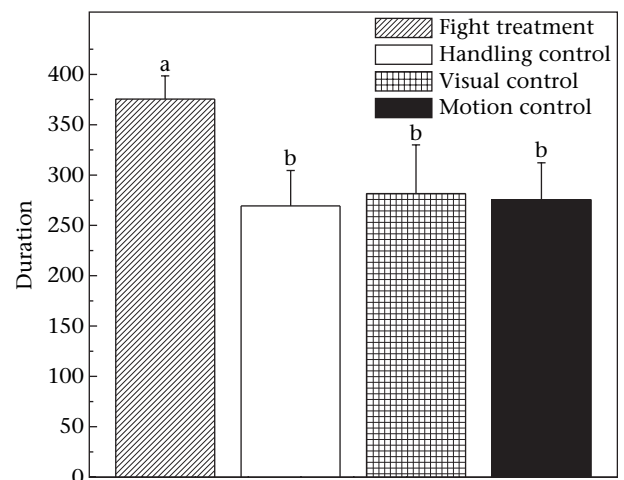


Figure 3. Mean + SE duration of subsequent fights for watcher individuals per treatment. Treatments that do not share letters (a, b) were significantly different, while treatments that share letters were not significantly different ($P < 0.05$).

visual control was compared with the handling and motion controls. This same pattern was found when the handling and motion controls are compared to each other (Fig. 3).

We can estimate the level of aggression by the rate of escalation of fights. This is measured by the amount of time crayfish interactions take to reach increasing levels of intensities. Thus, we statistically analysed the amount of time that each of the fights took to reach aggressive intensities of 2, 3 and 4. As in the previous measures, bystander crayfish, exposed to the fight treatments, reached intensity 2 at a significantly slower rate than bystander crayfish exposed to the handling, visual and motion controls ($P = 0.002$, $P = 0.006$, $P = 0.015$, $P < 0.05$, respectively; Fig. 4). There were no significant time differences between bystander crayfish exposed to the handling, visual or motion controls. Additionally, while using the same comparisons, bystander crayfish, exposed to the fight treatments, reached intensity 3 at a significantly slower rate than the other three treatments ($P = 0.03$, $P = 0.02$, $P = 0.02$, $P < 0.05$, respectively). As observed previously, there were no significant differences in latency to reach intensity level 3 in the three control experiments. There were no significant differences in any of the conditions for latency to reach intensity 4.

DISCUSSION

Contrary to our predictions, our results show that watching fights significantly alters the subsequent social behaviour of the bystander in a negative fashion. Since we fought the bystander against a naïve crayfish, this effect was independent of any winner or loser effect or information gain on the fighting abilities of subsequent opponents. Bystander crayfish that visually observed agonistic encounters were negatively affected in the subsequent interactions by having decreased winning and

initiation percentages. Fights with bystander crayfish that watched agonistic interactions were longer than the control fights. In addition, bystander crayfish that visually experienced the fight treatment were slower to escalate in the subsequent fights than crayfish in the control treatments. During a fight, the bystander crayfish took longer to reach fighting intensities 2 and 3. In summary, crayfish that observe an agonistic encounter do not initiate fights as often, have a slower rate of escalation, and take longer to end fights. Finally and most importantly, crayfish lose more often after observing prior agonistic interactions.

Our results show that being in the visual presence of another fight influences the outcome of subsequent social interactions. The role of visual signals in shaping crayfish aggression has rarely been investigated (Bruski & Dunham 1987). Visual cues are important under well-lit conditions in laboratory settings. In particular, crayfish showed visually mediated behaviours under conditions where light was not limited. These behaviours included tail flipping or retreat by subordinate animals when dominant animals approached or displayed (Bruski & Dunham 1987). When light was limited, these behaviours were less evident, suggesting that visually localizing the presence of a dominant crayfish is important for subordinates. In addition, changes in visual information appear to alter fight dynamics, such as the number and type of behaviours or the level of aggression (Bruski & Dunham 1987). Although there is a lack of detailed work on visual information and crayfish aggression, observing visual agonistic displays clearly influenced the behaviour of the bystander, presumably as a result of information gained by observing the encounter. Since the bystander was fought against a naïve individual, the change in behaviour observed in the bystander does not seem to be related to information about the fighting ability of the current opponent and may therefore be due to priming or reverse priming in the bystander.

Interestingly, results obtained in this study are opposite of those found in similar trials performed with vertebrates. In Siamese fighting fish, *Betta splendens*, and Mozambique tilapia, *Oreochromis mossambicus*, aggression appears to be heightened after observing social interactions and this leads to success in the subsequent agonistic encounters (Clotfelter & Paolino 2003; Oliveira et al. 2001, respectively). It is thought that, as a result of observing aggressive interactions, aggression in these fish is altered through hormonal changes and that winning is due to increased androgen levels. In addition, more recent work has shown that watching fights does not alter the subsequent behavioural response in green swordtail fish, *Xiphophorus helleri* (Earley et al. 2005). Priming, defined as an increase in hormones or neurotransmitter function associated with increased aggression (Oliveira et al. 2001), may be important in explaining results of previous work on vertebrates, in which success increased after watching social interactions. Yet, the prediction from this hypothesis does not fit this invertebrate model or the results presented in this study since dominance and aggression appear to be decreased in crayfish. Thus, it appears as if these concepts of priming are not applicable within this species.

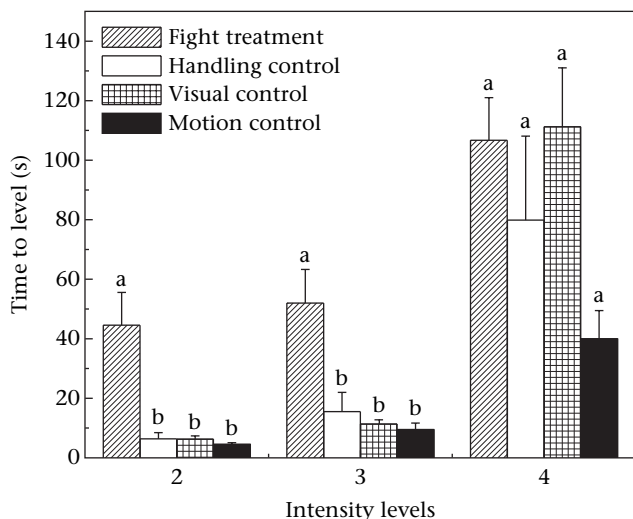


Figure 4. Mean + SE latency to intensity level of watcher fights for each treatment. Treatments that do not share letters (a, b) were significantly different, while treatments that share letters were not significantly different ($P < 0.05$).

Conversely, 'reverse priming', defined as a decrease in hormonal or neurotransmitter function, is a behavioural phenomenon where the bystander individual shows decreased aggression and potential to win encounters (Earley et al. 2005). (It is important to note that hormones or neurotransmitters could actually increase in function, but still down-regulate the aggressive behaviour. An example of this would be the impacts of androgen versus stress hormones in vertebrates.) It is possible that being in the visual presence of an agonistic encounter could alter the levels of hormones, increase stress, or alter the action of serotonin within the nervous system of crayfish (Edwards & Herberholz 2006). In particular, studies have shown that serotonin levels in crayfish can be modulated by a number of different situations, such as previous experience, social context and sensory stimuli (Huber et al. 1997; Huber & Delago 1998; Edwards & Herberholz 2006). Although speculative, it is possible that observing fights could alter the stress level of the bystander crayfish, which could decrease the functioning of serotonin in the bystander crayfish (Chang et al. 1999). A decrease of serotonin functioning leads to a reduction of aggression and subsequent losses in aggressive interactions (Edwards & Herberholz 2006). Although many researchers have focused on serotonin (Edwards & Kravitz 1997; Huber et al. 1997; Huber & Delago 1998), other physiological mechanisms associated with stress such as alterations of levels of other circulating hormones could account for the effects seen in this study.

In addition to 'reverse priming' as a possible explanation, the role of communication in crayfish interactions could also provide an explanation for the results presented here. Crayfish use chemical signals as sources of information during social interactions to determine whether to escalate aggression (Moore & Bergman 2005), as information for determining winners and losers (Bergman et al. 2003), and in regulating subsequent aggression and dominance (Daws et al. 2002). In addition, long-term exposure to chemical signals has the potential to alter subsequent social behaviour (Bergman & Moore 2005). All of these studies point to the important role that chemical signals play as sources of information during social interactions. When the ability to release chemical signals is experimentally removed from an individual crayfish, this process has negative social consequences (Zulandt-Schneider et al. 2001). It is possible, but untested, that the bystander crayfish in our studies is releasing chemical signals during the observational stage of the experiment. Consequently, the bystander crayfish may not have enough reserves of chemical signals to use during subsequent encounters. The lack of ability to use appropriate chemical signals during a subsequent interaction would lead to a decrease in aggression, slowed escalation and negative fight outcomes (Zulandt-Schneider et al. 2001). Recent work on urine release (Bergman et al. 2005; Simon & Moore 2007) has shown that urine release during social interactions is often carried out in conjunction with specific behaviours and is often quite limited in duration. These results are consistent with the possible depletion of urine during the observational phase of this experiment.

Given that our results indicate a negative fitness consequence for observing social interactions (such as

potential loss of shelters and mates), it is reasonable to ask 'why do crayfish watch?' Note that the bystander crayfish fought naïve opponents and perhaps this 'new' participant is a context that is inappropriate for the evolution of this behaviour in the field. It is possible that the benefits of observing social interactions, in terms of increasing information quality about the observed antagonists, outweighs the costs of interacting with an individual that you are not prepared to fight against. More recent work on social behaviour has shown that factors that influence crayfish social behaviour are indeed context dependent (Fero et al. 2007). It is possible that observation changes the neuroendocrine milieu in ways that actually increase the bystander's ability to discriminate the fighting abilities of certain opponents. When taken out of context (i.e. interacting with an unknown naïve animal), observation could represent a disadvantage in terms of an observer's inability to apply the acquired knowledge to subsequent social interactions.

Another possible explanation for the potentially negative fitness consequences of our findings implies differences in priming and reverse priming effects. For example, priming might be favoured within some contexts because, when an animal observes nearby aggressive interactions, this might indicate an increased probability that the bystander will need to defend the valuable or scarce resources it currently holds against an intruder. In this instance, it would benefit the bystander to up-regulate its own aggressive motivation when there are lots of nearby fights so it can respond more rapidly or forcefully to an intruder. Conversely, when there are lots of nearby fights, and the resources defended are not particularly valuable or are abundant, it may pay for a bystander to down-regulate its own aggressive motivation. Given that there is a high probability that the bystander will be challenged, and given that fighting is costly, it may pay to avoid escalation when challenged. Again, the impacts of these explanations on the social behaviour of the crayfish would be context dependent.

Crayfish are very mobile in nature and the role of previous social experiences, including repeated encounters with the same individual or being within the presence of encounters, is not well documented. The role of visual, chemical and mechanical signals in natural habitats needs to be addressed and, in particular, the role of information in guiding the structuring of social hierarchies needs to be investigated. Crayfish habitats include fast running streams that can be muddy or swampy, which may limit the effective distances of visual and chemical signals. Many crayfish species are nocturnal, which may further limit the usefulness of visual signals; yet the results presented here indicate that visual signals have the ability to alter the subsequent social dynamics. With a plethora of factors that influence aggression and dominance in crayfish, it is unknown how these factors interact together to produce dominance and to structure social systems. In the field, it may be possible that crayfish determine subsequent agonistic strategies from the information gathered during nonfighting situations through a number of sensory channels. If this is the case, then, visual signals paired with chemical signals may result in

increases in social success as seen in other eavesdropping experiments.

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