Hierarchical decision making: resource distribution exhibits stronger effect on crayfish dominance relationships and shelter occupation than prior social experience and resource ownership

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Abstract

The outcome of agonistic interactions is critical to the acquisition of vital resources. These behaviours can be influenced by several intrinsic and extrinsic factors, and multi-faceted studies are necessary for ecologically relevant studies. The aim of this study was to combine the effects of past social experience, resource ownership, and the distribution of shelter resources to examine the combination of these effects on various measures of agonism in crayfish (\textit{Orconectes rusticus}). Crayfish were assigned to one of three social conditioning treatments (naïve, subordinate, dominant) and then introduced to an arena where they were assigned to a resident or intruder treatment. An intruder shelter was then positioned 20, 60 or 120 cm from the resident shelter. We found that resource distribution (shelter distance) played a larger role in influencing agonistic behaviour than did past social experience or current social status.

Keywords

crayfish, dominance, prior residence, resource ownership, shelter, social status, status reversal.

1. Introduction

Agonistic behaviour has long been established as behaviour necessary for many animals to obtain vital resources such as shelter, food, and mates (Parker, 1974; Smith & Parker, 1976). However, fighting behaviour incurs costs on individuals in the form of energy depletion, time lost from foraging...
or mating, and potential injury or death (Parker, 1974; Parker & Rubenstein, 1981). Therefore, game theory predicts that several factors should be considered before animals engage in resource driven fighting behaviour. Two major factors that appear to contribute to fight outcome and consequent resource acquisition are resource holding potential (RHP) and the subjective value that animals place on a given resource (Hurd, 2006; Arnott & Elwood, 2009).

RHP is a multi-faceted and complex approximation of an individual’s ability to obtain a resource (Parker, 1974). RHP is studied in the context of body size or weight and weaponry size, and an individual with greater RHP (e.g., body size or weight) is more likely to win an encounter (squid: DiMarco & Hanlon, 1997; copperhead snakes: Schuett, 1997; swordtail fish: Prenter et al., 2008). RHP is also influenced by physiological factors such as available energy stores, the build-up of metabolites during contests, and hormonal fluctuations (Briffa & Elwood, 2005; Oliveira, 2009). In a study of shell fighting in hermit crabs (Pagurus bernhardus), Briffa & Elwood (2005) found that relative glucose (available energy) and glycogen (metabolite build-up) levels greatly affected the fight duration for both attackers and defenders. These intrinsic factors can affect current contests as well as performance in and the outcome of future contests. Mangrove killifish (Kryptolebias marmoratus) adjust consequent contest decisions and strategies after wins and losses depending on the hormonal state after the win or loss (Earley et al., 2013). Individuals with levels of hormones that corresponded to lower relative aggression (and consequently a reduced likelihood of winning a contest) were more likely to alter their future contest decisions after a previous fight (win or lose). The impacts of previous experiences on future contests are known as ‘winner’ and ‘loser’ effects. These effects correspond to a higher probability that previous winners continue winning and losers continue losing (Hsu & Wolf, 1999; Mesterton-Gibbons, 1999; Dugatkin & Druen, 2004). While internal mechanisms such as metabolite build-up and hormonal fluctuations can play a role in future experiences, previous contest experience can also influence RHP through more accurate knowledge of one’s own strength or fighting ability (Fawcett & Johnstone, 2010). As accuracy in knowledge of strength increases, an individual can make less risky decisions about when to fight and when to retreat.

Resource value (RV) also plays an important role in fighting behaviour and contest outcome. Each contestant involved in a fight has different energetic and survival driven needs and, consequently, places different values on
any given resource. Furthermore, not all resources are equal. More desirable food, shelters, and mates are highly sought after and highly contested (Lindstrom & Pampoulie, 2004; Goubalt et al., 2007; Arnott & Elwood, 2008). Distribution of resources is one factor that influences the RV in the sense that resources with the same inherent quality may differ with regard to defensibility, how costly they are to obtain, and/or the patchy nature of resources. For example, clumped resources are easier to defend and less vulnerable to competing individuals (Robb & Grant, 1998; Noël et al., 2005). Prior ownership of a resource can also skew subjective resource value. Prior residence can increase the RV of the shelter for the owner due either to energy used previously to build or obtain the shelter (Lindstrom & Pampoulie, 2004) or more accurate knowledge of the value of the shelter compared to an intruder (Arnott & Elwood, 2008). Hermit crabs exhibit prior residency advantages in which shelter owners tend to win more fights than intended usurpers. In this study, the authors suggest that longer tenure of residency in a given shelter adds even more value due to the establishment of neighbour boundaries, reducing neighbour–neighbour fighting (Fayed et al., 2008).

The objective of this study was to investigate how previous social experience, prior residence, and resource distribution interact to influence an individual’s ability to control resources through fighting behaviour and establishment of dominance. Due to the extensive studies performed on factors impacting dominance establishment in crayfish (Levenbach & Hazlett, 1996; Stocker & Huber, 2001; Bergman & Moore, 2003; Martin & Moore, 2008; Zulandt et al., 2008), this study focused on answering these questions in the crayfish Orconectes rusticus.

2. Methods

2.1. Animals

Crayfish (Orconectes rusticus) were collected from the Portage River, Wood County, OH, USA in the autumn of 2007. Form I (reproductive) males were measured for carapace length (beginning of the rostrum to the end of the cephalothorax) (mean ± SEM; 3.2 ± 0.03 cm) and chelae length (3.0 ± 0.04 cm). Crayfish were housed in flow-through plastic containers that visually and chemically isolated them from one another. All crayfish were isolated for a minimum of seven days in order to eliminate effects of prior social history (Zulandt-Schneider et al., 2008). Crayfish were maintained on
a 12 h:12 h light/dark cycle and were fed a diet of commercial rabbit food pellets which were distributed to each individual three times per week. Only crayfish with intact appendages were used in experiments, and each individual was only used once. Prior to the beginning of the experimental protocol, crayfish were marked with reflective tape on the dorsal portion of the carapace or chelae in order to differentiate between individuals during trials. Only intermoult individuals were used in this experiment in order to control for moult status. Any individuals that moulted 1 week prior to, during, or 1 week after the experiment were excluded from analysis.

2.2. Experimental design

The experiment was designed as a \(3 \times 3\) factorial design (72 total trials, \(N = 8\) for each status \(\times\) distance treatment) with three social status treatments (dominant, subordinate, and naïve) and three shelter distance treatments (20, 60 and 120 cm). Each social status treatment was comprised of twenty four crayfish and body size did not differ across these groups ((treatment: carapace, chelae) naïve: 3.1 ± 0.1 cm, 2.9 ± 0.1 cm; dominant: 3.2 ± 0.1 cm, 3.0 ± 0.1 cm; subordinate: 3.1 ± 0.1 cm, 2.8 ± 0.1 cm). Distance treatments were chosen based on nearest neighbour distances recorded in the field for *Orconectes propinquus* (Fero & Moore, 2008) in order to create a context of ecological relevance. Prior to experimental trials, crayfish (focal individuals) underwent conditioning for social status and shelter residency over the course of two days (described below). At the end of the second day, a conditioned focal crayfish (further referred to as ‘resident’) was introduced to an arena with a size-matched, naïve conspecific (further referred to as ‘intruder’) and an additional shelter (Figure 1). Subsequent agonism and shelter use was observed (details below).

2.3. Social status and residency conditioning

Studies have shown that previous and repeated winning or losing experiences can have prolonged effects on future agonistic interactions (Daws et al., 2002; Fero et al., 2007). To produce individuals with differing social status, focal crayfish were subjected to a social status conditioning protocol in which the focal crayfish was paired with a ‘conditioning’ crayfish of a 10–30% size difference (carapace and chelae). Size asymmetries in crayfish are highly predictive of fight outcome (Bovbjerg, 1953; Garvey & Stein, 1993), and the range of size differences used in this experiment allows for manipulation of outcome while ensuring that crayfish still engage each other in
Figure 1. Set up for pre-conditioning trials for social experience (subordinate, dominant, naïve) and resident status as well as experimental trials. Focal crayfish were first subjected to social conditioning fight trials (top left corner) via pairing with an individual that was 10–30% smaller (focal is dominant) or 10–30% larger (focal is subordinate). Naïve focal crayfish were placed in the tank but never interacted with another individual. These trials lasted for 40 min and were performed over the course of 48 h with three conditioning trials taking place per day. When focal animals were not engaged in social conditioning trials, they were placed in the experimental arena (top right corner) with a shelter to establish ownership of the shelter. At the conclusion of the 48-h pre-conditioning period, focal crayfish were placed in the experimental arena with their shelter along with a size-matched naïve ‘intruder’ crayfish. After a 20-min acclimation period for both crayfish, experimental trials ran for 24 h.

agonistic interactions. In order to produce dominant and subordinate individuals in the pre-conditioning phase, focal crayfish in the dominant status treatment were paired with a conditioning crayfish that was 10–30% smaller (focal wins) and focal crayfish in the subordinate treatment were paired with a conditioning crayfish that was 10–30% larger (focal loses). Intruder crayfish were not given a socially conditioned status prior to contact with the focal (resident) crayfish.

Focal and conditioning crayfish were placed in a 20-l aquarium with a divider between them to prevent interaction. After a 20-min acclimation period, the divider was removed and the dyad was allowed to interact for
Shelter distribution, social experience influences dominance

20 min. Agonistic behaviour was videotaped and analysed using an ethogram adapted from Bruski & Dunham (1987) (cf., Bergman & Moore, 2005). Conditioning was performed over the course of two days with three conditioning trials per day, separated by at least 1 h. This protocol has been shown to yield status-specific differences in behaviours (Fero et al., 2007). Pairs in which dominance relationships were not clearly established or reinforced during each conditioning trial were not used in experimental trials. Naïve treatment individuals were subjected to the same handling protocol, except they were not exposed to conspecifics during the conditioning phase.

When focal crayfish were not engaged in a conditioning trial, they were placed in the experimental arena in order to generate a ‘prior residence effect’ (Figure 1). Previous studies have shown that crayfish that were exposed to a shelter for 24 h in the absence of a conspecific were subsequently more likely to win agonistic encounters (Peeke et al., 1995). While body size asymmetries in male Orconectes rusticus are more predictive of fight outcome (Martin & Moore, 2008), prior residence has yet to be shown to affect agonism among size-matched individuals.

2.4. Experimental arena

The experimental arena consisted of a 1.8 m diameter pool containing one shelter (halved 7.5 cm diameter PVC pipe, 11.0 cm long) and black pumice substrate to aid in visualization of crayfish. White and red lamps were mounted around the perimeter of the pool in order to maintain a consistent L–D cycle, and red lights were left on continuously so that crayfish were visible during dark periods. A surveillance camera (model CVC-6993CL) was mounted approx. 1.5 m above the pool in order to record crayfish behaviour. Video was captured at one frame per three seconds on a time lapse video recorder (Samsung SSC-960 and Sylvania SY96R).

2.5. Experimental protocol

Following the last conditioning trial, the focal crayfish (resident) was placed into the testing arena and confined in its shelter (resident shelter) by a weighted cage constructed from egg crating. A size-matched, naïve crayfish (intruder) with no prior social conditioning was also confined to a shelter (intruder shelter) which was placed at 20, 60 or 120 cm away from the resident shelter to demonstrate varied resource distribution. Naïve intruders were not socially conditioned and had no contact with conspecifics or experimenters.
for at least seven days prior to introduction into the experimental arena in order to erase any effects of prior social experiences (Karavanich & Atema, 1998). Crayfish remained confined in their respective shelters for a 20-min acclimation period, at the end of which experimental trials commenced by lifting the shelter cages and allowing crayfish to move freely for 24 h (Figure 1). At the end of the 24-h trial, both crayfish were removed from the arena, which was drained, refilled, and then aerated for at least 12 h prior to beginning the next experiment.

2.6. Data analysis

Video recordings underwent blind analysis, in which agonism (number of encounters) and shelter use were quantified. The number of agonistic encounters was determined using the same ethogram as in social conditioning trials (Bergman & Moore, 2005). An encounter began with an approach by one individual and ended with a retreat followed by a 10-s absence of interaction and spatial separation of two body lengths. The dominance status the resident crayfish acquired during experimental trial (trial status) was also recorded. Dominance status was described as a ‘reversal’ if the resulting ‘trial status’ was different than the resident’s ‘conditioned status’. The proportion of trials in which reversals occurred, as well as the proportion of trials where the resident was dominant to the naïve intruder were calculated.

Different measures were used to determine shelter ownership and control. Social interactions were considered ‘shelter-related’ if they occurred within two body lengths of a shelter and were not associated with a shelter eviction. Crayfish shelter occupancy began when a crayfish was completely obscured by the shelter and ended when the individual moved more than one half body length away from the shelter. Evictions occurred when a shelter occupant was displaced from the shelter by the other crayfish. Crayfish approaches within one body length of a shelter without entering the shelter were also recorded and considered a possible indicator of ownership. Additionally, percent of shelter entries were calculated (No. of shelter entries into shelter X/(No. of shelter approaches to shelter X + entries into shelter X)). Descriptions of behavioural measures are summarized in Tables 1 and 2.

A multiple comparisons for proportions contingency table (Zar, 1999) was used to compare the effects of conditioned status and shelter distance on the occurrence of resident status reversals and resident dominance. The proportion of naïve treatment residents that were dominant to intruders in
Table 1.
Definitions and descriptions of agonistic behaviours and shelter use utilized for data analysis in these trials.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agonistic encounter</td>
<td>Begins with approach within one body length; ends with retreat (e.g., tail flip) and separation by 2 body lengths.</td>
</tr>
<tr>
<td>Shelter-related encounter</td>
<td>Agonistic encounters occurring within 2 body lengths of a shelter (including evictions).</td>
</tr>
<tr>
<td>Shelter entry</td>
<td>Crayfish enters a shelter and is completely obstructed from view.</td>
</tr>
<tr>
<td>Shelter occupancy</td>
<td>Begins with shelter entry and ends when the crayfish moves 1/2 body length away from the shelter.</td>
</tr>
<tr>
<td>Shelter eviction</td>
<td>Crayfish leaves a shelter in direct response to an agonistic encounter.</td>
</tr>
<tr>
<td>Shelter approach</td>
<td>Crayfish comes within one body length of a shelter without entering.</td>
</tr>
<tr>
<td>Percent shelter entries</td>
<td>Number of entries into shelter X/(Number of approaches to shelter X + Number of entries into X).</td>
</tr>
<tr>
<td>Status reversal</td>
<td>Social status of the focal resident relative to the naïve intruder is opposite of that predicted by status conditioning.</td>
</tr>
</tbody>
</table>

Experimental trials was compared across distance treatments and against an expected random value of 50% in order to determine whether a prior residence effect was present. MANOVAs with Tukey post-hoc analyses were used to examine the interaction between conditioned status (dominant or subordinate), shelter distance (20, 60 or 120 cm), trial status (dominant or subordinate), and the extent to which these factors predicted the number of agonistic encounters, shelter use, and shelter control. All proportions were arcsine transformed for statistical analyses (Zar, 1999). MANOVAs were performed with Statistica software, version 6.0 (StatSoft, Tulsa, OK, USA).

3. Results

3.1. Dominance relationships

3.1.1. Resident dominance
The likelihood of a resident being dominant to an intruder was dependent upon the distance between shelters ($\chi^2 = 16.39, p < 0.05; q_{0.05, \infty, 9} = 4.39$). Naïve and dominant-conditioned residents were dominant to intruders more often when shelters were farther apart. Naïve residents were dominant to
Table 2.

<table>
<thead>
<tr>
<th>Intensity level</th>
<th>Behaviour description</th>
</tr>
</thead>
<tbody>
<tr>
<td>−2</td>
<td>Tailflip away from opponent or fast retreat.</td>
</tr>
<tr>
<td>−1</td>
<td>Retreat by slowly backing away from opponent.</td>
</tr>
<tr>
<td>0</td>
<td>Visually ignore opponent with no response or threat display.</td>
</tr>
<tr>
<td>1</td>
<td>Approach without threat display, walking slowly towards opponent.</td>
</tr>
<tr>
<td>2</td>
<td>Approach with meral spread threat display with the major chelae; antennal (2nd antennae) whips are present, often with maxillipeds creating currents. Antennules (1st antennae) often are seen flicking.</td>
</tr>
<tr>
<td>3</td>
<td>Initial major chelae use by boxing, pushing, and/or touching with closed chelae. Chelae are not used to grasp but can be opened and pushed. Antennal whips are more vigorous. Antennule (1st antennae) flicking not seen.</td>
</tr>
<tr>
<td>4</td>
<td>Active major chelae use by grabbing and/or holding opponent. Crayfish will try to turn opponents over or physically manipulate them, generating force through active major chelae use.</td>
</tr>
<tr>
<td>5</td>
<td>Unrestrained fighting by pulling at opponent’s chelae or body parts. Opponents try to pull or tear legs, antennae, or major chelae off of individuals.</td>
</tr>
</tbody>
</table>

Description of behaviours (right column) correspond to a numerical representation of that behaviour (left column) used in data analysis.

intruders in significantly more of the 120-cm trials (7 out of 8) than in the 20-cm trials (3 out of 8) ($q_{0.05,\infty,9} = 5.63; p < 0.05$) (Figure 2). Dominant-conditioned residents were dominant to intruders in a significantly higher proportion of both 60-cm and 120-cm trials (7 out of 8 in each) compared to 20-cm trials (3 out of 8) (60 cm: $q_{0.05,\infty,9} = 5.63$; 120 cm: $q_{0.05,\infty,9} = 5.63$; $p < 0.05$) (Figure 2).

Subordinate-conditioned residents exhibited different dominance outcomes during experimental contests than those observed for dominant-conditioned and naïve resident treatments. Subordinate-conditioned residents were dominant to intruders in experimental contests more often at shorter shelter distances. Dominance by subordinate-conditioned residents was established in significantly fewer of the 120-cm trials (2 out of 8) compared to 60-cm trials (6 out of 8) and proportion of dominance in 60-cm trials did not differ from 20-cm trials (4 out of 8) (60 cm: $q_{0.05,\infty,9} = 5.42$, $p < 0.05$; 20 cm: $q_{0.05,\infty,9} = 2.71$, $p > 0.05$) (Figure 2). Prior social conditioning alone did not predict resident dominance. When inter-shelter distance is not considered, residents were dominant to intruders in the same
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Figure 2. Proportion of trials in each treatment (conditioned status × inter-shelter distance) where focal residents were dominant to naïve intruders. Hatched bars represent 20-cm inter-shelter distance treatments; grey bars represent 60-cm treatments; black bars represent 120-cm treatments. The likelihood of a resident being dominant to an intruder was dependent upon the distance between shelters ($\chi^2 = 16.39$, $p < 0.05$; $q_{0.05,\infty,9} = 4.39$). Letters above the bars differ when bars are significantly different from each other.

proportion of total trials across social conditioning treatments ($\chi^2 = 2.19$, $p > 0.05$; $q_{0.05,\infty,3} = 3.31$).

3.1.2. Status reversals
Both dominant- and subordinate-conditioned residents exhibited reversals in dominance status when presented with a naïve intruder. The likelihood of a reversal (deviation from expected dominance relationships) was dependent upon the distance between shelters ($\chi^2 = 11.94$, $p < 0.05$; $q_{0.05,\infty,6} = 4.03$) (Figure 3). A significantly higher proportion of reversals was observed for conditioned dominants in the 20-cm treatment (5 out of 8) versus 60-cm and 120-cm treatments (1 out of 8 in each) (60 cm: $q_{0.05,\infty,6} = 5.63$; 120 cm: $q_{0.05,\infty,6} = 5.63$; $p < 0.05$) (Figure 3). In other words, the probability of a reversal of dominance status decreased as inter-shelter distances increased. Similarly, the probability of a subordinate reversal increased as inter-shelter distances decreased (4 out of 8, 6 out of 8 and 2 out of 8 for the 20-, 60- and 120-cm trials, respectively) (60 cm: $q_{0.05,\infty,6} = 5.42$, $p < 0.05$; 20 cm:
Figure 3. Proportion of dominant and subordinate status condition trials where dominance reversals occurred. Reversals are defined as resident/intruder dominance relationships that deviate from those predicted by status conditioning. Hatched bars represent 20-cm inter-shelter distance treatments; grey bars represent 60-cm treatments; black bars represent 120-cm treatments. The occurrence of reversals depended on inter-shelter distance ($\chi^2 = 11.94, p < 0.05$; $q_{0.05, \infty, 6} = 4.03$). Letters above the bars differ when bars are significantly different from each other.

$q_{0.05, \infty, 6} = 2.71, p > 0.05$) (Figure 3). Thus, social conditioning accurately predicted reversals in status of resident/intruder dominance relationships only when shelters were farther apart from each other (60 cm and 120 cm).

3.1.3. Agonism

Agonistic encounters in close proximity to a shelter were significantly more likely to occur near the resident shelter (52% of fights) than near the intruder shelter (32% of fights; 16% of fights occurred at a distance from either shelter) (MANOVA; $F_{(1,126,0.05)} = 14.72, p < 0.001$). The proportion of fights that were shelter-related was equal across all treatments (MANOVA (distance × conditioned status); $F_{(4,63,0.05)} = 0.86, p = 0.49$). The total number of agonistic encounters observed were also similar across conditioned status and distance treatments (MANOVA; $F_{(4,63,0.05)} = 1.06, p = 0.38$). Crayfish engaged in more fights around the resident shelter and neither inter-shelter
distance nor resident social conditioning affected the overall occurrence of agonism.

The occurrence of shelter evictions was strongly related to resident/intruder dominance relationships. The majority of shelter evictions were performed by pre-conditioned dominant residents with the exception of two trials (2 out of 24), which were performed by pre-conditioned subordinate residents. No effect of inter-shelter distance on shelter eviction occurrence was observed (MANOVA; \( F_{(2,29,0.05)} = 0.23, p = 0.79 \)). Additionally, both residents and intruders evicted individuals from both resident and intruder shelters evenly (MANOVA; resident: \( F_{(2,46,0.05)} = 2.71, p = 0.08 \); intruder: \( F_{(1,52,0.05)} = 0.93, p = 0.34 \)).

3.2. Effect of social status and inter-shelter distance on shelter use

3.2.1. Residents

Inter-shelter distance significantly influenced shelter approaches by resident crayfish (MANOVA; \( F_{(2,126,0.05)} = 3.29, p < 0.04 \)). Residents approached resident shelters (8 \( \pm \) 0.6 approaches) significantly more often than intruder shelters in 60-cm (2 \( \pm \) 0.3 approaches) distance treatments (Tukey post-hoc: \( p < 0.01 \)). Resident and intruder shelters were approached an equal proportion of times at 20 cm and 120 cm by both residents and intruders (20 cm: 9.1 \( \pm \) 0.63 approaches for resident shelter by resident crayfish; 9.7 \( \pm \) 0.7 approaches for intruder shelter by resident crayfish; 9.4 \( \pm \) 0.91 for resident shelter by intruder crayfish; 6.3 \( \pm \) 0.72 for intruder shelter by intruder crayfish; 120 cm: 10 \( \pm \) 0.8 approaches for resident shelter by resident crayfish; 10 \( \pm \) 0.7 approaches for intruder shelter by resident crayfish; 10.2 \( \pm \) 0.7 for intruder shelter by intruder crayfish; Tukey post-hoc; 20 cm: \( p = 0.21 \); 120 cm: \( p = 0.99 \)). Both dominant- and subordinate-conditioned residents approached both shelters equally (MANOVA; conditioned status: \( F_{(2,126,0.05)} = 2.08, p = 0.13 \); trials status: \( F_{(1,132,0.05)} = 2.67, p = 0.11 \)). The proportion of shelter entries made out of total approaches (including entries) were also similar between resident and intruder shelters across status conditions and distance treatments (MANOVA; \( F_{(4,126,0.05)} = 1.02, p = 0.40 \)).

Both inter-shelter distance and trial status significantly predicted shelter occupation. Residents overall spent more time occupying the resident shelter in the 120-cm treatment (MANOVA; \( F_{(2,66,0.05)} = 3.15, p < 0.05 \)), and when residents were dominant to intruders (MANOVA; \( F_{(1,66,0.05)} = 14.45, p = 0.0003 \)).
Both resident and intruder shelters were occupied equally with regard to conditioned status (MANOVA; $F_{(2,63,0.05)} = 2.45$, $p = 0.09$). Additionally, no significant interaction between distance and trial status was observed (MANOVA; $F_{(2,66,0.05)} = 0.93$, $p = 0.39$). Resident crayfish overall spent a larger proportion of time in the resident shelter (MANOVA; $F_{(1,126,0.05)} = 11.13$, $p < 0.001$).

3.2.2. Intruders
Approaches to the resident shelter by intruders in experimental trials differed depending on inter-shelter distance (MANOVA; $F_{(2,126,0.05)} = 8.50$, $p < 0.001$). At 20 cm, intruders approached the resident shelter significantly more often than intruder shelters ($9.4 \pm 0.91$ for resident shelter and intruder crayfish and $6.3 \pm 0.72$ for intruder shelter and intruder crayfish) (Tukey post-hoc; $p < 0.001$). As inter-shelter distance increased, resident and intruder shelters were approached evenly by intruders (120 cm: $p = 0.46$).

Dominant and subordinate intruders differed in the percent of entries made between resident and intruder shelters (MANOVA; $F_{(1,132,0.05)} = 9.73$, $p < 0.005$). Dominant intruders entered both the resident and intruder shelter equally (Tukey post-hoc, $p = 0.95$), but subordinate intruders entered the intruder shelter significantly more than resident shelter ($11.3 \pm 0.4$ for intruder shelter entries and $7.7 \pm 0.61$ for resident shelter entries) (Tukey post-hoc, $p < 0.001$). Dominant and subordinate intruders also differed in the percentage of shelter approaches that resulted in entries to shelter overall (MANOVA; $F_{(1,132,0.05)} = 13.24$, $p < 0.001$). Dominant intruders entered and approached shelters more often than subordinate intruders ($13 \pm 0.8$ for dominant intruders and $6.8 \pm 0.32$ for subordinate intruders) (Tukey post-hoc; $p < 0.001$). Intruders overall spent an equal proportion of time in resident versus intruder shelters (MANOVA; $F_{(1,132,0.05)} = 0.05$, $p = 0.82$).

4. Discussion
In this study, interactive effects between prior social experience, resource ownership, and resource distribution were studied and quantified. Furthermore, these effects were examined in light of their impact on the ability of individuals to control resources and compete in aggressive contests. We found that the distance between shelters exhibited the strongest influence over fight outcomes and, consequently, the formation of dominance relationships. As inter-shelter distance increased, social conditioning and prior
residence effects became more predictive of resident/intruder dominance relationships (Figure 2).

In the 20-cm distance treatment, subordinate-conditioned residents’ odds of being dominant to the intruder were no better than random while naïve and dominant-conditioned residents were slightly more likely to lose to intruders. Meanwhile, 60-cm trials saw naïve residents with equal chances of being dominant or subordinate to intruders and a very high proportion of both dominant and subordinate residents showing dominance over intruders. Finally, large distances between shelters (120-cm treatment) showed a high probability of residence dominance for naïve and dominant-conditioned residents and a very low probability of dominance for subordinate-conditioned residents (Figure 2). Taken together, these data imply that crayfish likely have some type of ‘decision making hierarchy’ in place that is dictated first by distance of interaction from the home shelter then by prior experience and resource ownership.

As the distance between resources increases, the subjective resource value (RV) of each resource is also likely to increase due to the scarcity of that resource and an increased competitor to resource ratio (Noël et al., 2005) imposed by the distance. This increased RV is especially true for a species (e.g., crayfish) that places high value on shelters in order to avoid predation (Bergman & Moore, 2003). Consequently, an area where high quality shelters are comparable in number to the number of crayfish, we expect to see low RV and the absence of prior social experience or resource ownership as an indicator of ability to obtain a resource. Indeed, at short distances we see subordinate individuals with an equal chance of being dominant or subordinate to intruders and naïve and dominant conditioned residents that are slightly more likely to be subordinate to intruders (Figure 2). As distance (and subsequently RV) increases, prior experience and/or resource ownership should play a greater role than distance in determining dominance relationships. Correspondingly, we see that any type of prior experience confers some type of advantage at 60 cm as both dominant- and subordinate-conditioned residents are dominant to intruders well over half of the time while naïve residents’ chances of obtaining dominance is no better than random (Figure 2). At the largest distance separation of the resources (120-cm treatment), RV is at its highest and prior experience and resource ownership should dictate dominance. This prediction is supported by our findings. In the 120-cm treatment, dominant-conditioned residents are significantly more
likely to be dominant to intruders while subordinate-conditioned residents are significantly more likely to be subordinate to intruders, implying a strong influence of winner and loser effects from previous interactions. The fact that naïve residents are also dominant to intruders significantly more often in the 120-cm treatment shows that some type of resident effect is also in place at increased shelter distances. These data show that while resource distribution, prior experience, and resource ownership interact to dictate dominance relationships and the ability to maintain control of a resource, a behavioural decision hierarchy exists in which distance between resources dictates the outcome of these interactions before the impact of prior experience or resource ownership.

The finding that prior social experience plays a minor role in resource acquisition and dominance relationships is curious as other studies have consistently found that this experience plays an integral role in both (Chase et al., 1994). Studies of prior social experience have revolved around the impact of winner and loser effects in which individuals with a prior winning or losing experience are more likely to win or lose, respectively, in subsequent interactions (Bergman et al., 2003; Dugatkin & Earley, 2004; Earley et al., 2013). These studies have taken place across several taxa and have consistently shown that loser effects are commonly more intense and longer lasting than winner effects (Bakker et al., 1989; Kasumovic et al., 2010). Hsu & Wolf (1999) hypothesize that the retention of these prior social effects is dependent on how often individuals in a particular species encounter other individuals and engage in agonistic behaviour. For instance, in larger populations with increased instances of aggressive encounters, individuals gain more frequent, and probably more reliable, information over short amounts of time (Mesterton-Gibbons & Heap, 2014). Therefore, it is highly probable that an individual with constant social interaction will retain neither information nor the effects of past encounters for long amounts of time (Bakker et al., 1989; Schuett, 1997). Previous studies in crayfish have shown the presence of both winner and loser effects (Bergman et al., 2003; Hock & Huber, 2006). However, prior social status played a small role in combination with prior residence effects and resource distribution in this study. This finding is consistent with the theoretical predictions made by applying Hsu and Wolf’s hypothesis about the effects of interaction frequency on winner and loser effects to crayfish ecology. Crayfish populations are made up of relatively large numbers of individuals (Momot et al., 1978; Huryn & Wallace, 1987;
Parkyn et al., 2002). Moreover, the spacing of shelters and patchiness of food distribution attracts large numbers of individuals to a single area (Bergman & Moore, 2003; Fero & Moore, 2008, 2014; Martin & Moore, 2008; Ranta & Lindström, 2010). Consequently, crayfish constantly experience social interactions (e.g., agonistic encounters), especially when resource patches are scarce or spread over greater distances. These frequent social interactions suggest that long term retention of information of agonistic encounters would be costly and inefficient for crayfish (Hsu & Wolf, 1999; Zulandt et al., 2008; Cook & Moore, 2009). Furthermore, the prevalence of clumped resources in crayfish habitat increases the likelihood of seeing the same results of our 20-cm treatment. Low resource value as a result of high shelter availability likely dilutes winner and loser effects, making any two physically matched individuals equally likely to obtain and control a resource.

As distance between resources increase (i.e., increased RV) loser and winner effects can also be influenced by contextual components surrounding a fight. Resident status (i.e., resource ownership) is one factor that can alter fight context and fight outcome (Fuxjager et al., 2009). Prior residence played a noticeable role in concert with prior experience in the 120-cm distance treatment (Figure 2), but was still secondary to resource distribution in effect on resource control and dominance relationships. Residency commonly confers an advantage to residents over intruders (Sacchi et al., 2009). This advantage is due either to the fact that owners commonly have higher innate RHP that allows them to accumulate resources (Kokko et al., 2006) or because a resident individual has more accurate information about the resource value of the shelter compared to the intruder (Smith & Parker, 1976). In male lizards (*Podarcis muralis*) residency conferred a large advantage. Although larger males were generally more aggressive than small males and were successful in fights with large size asymmetries, the residence asymmetry appeared to favour smaller individuals as smaller individuals nearly tripled their success rates in combat with residents (Sacchi et al., 2009). Ranta & Lindström (1993) found similar results to Sacchi et al. (2009) in signal crayfish (*Pacifastacus leniusculus*). In instances where shelters were limited, larger individuals were better at obtaining a shelter. However, if a small individual established residency the individual was much more likely to fend off large opponents for that resource (Ranta & Lindström, 1993). In this study, pre-established resource ownership influenced resident (focal animal) dominance over intruders, the occurrence of agonism, and shelter evictions and approaches. However, these effects were highly dependent upon
inter-shelter distance (Figure 2). As mentioned previously, crayfish tend to live in larger populations. Due to limited space to build burrows or a limited amount of rocks or crevices that can provide shelter (Bovbjerg, 1970; Hill & Lodge, 1999), multiple crayfish can be found in each ‘residence’ (Alonso & Martínez, 2006). The necessity to share limited resources, especially during rapid escape from predators, may dilute the potency of prior residence effects in some crayfish species.

In summary, our results support a hierarchy of decision making that determines dominance relationships and resource acquisition in crayfish. Resource distribution played an integral role in hierarchy establishment and resource allocation in this study while prior experience and resource ownership exhibited secondary effects. Notably, as inter-shelter distances increased, prior experience and resource ownership dictated resource control and dominance relationships. Furthermore, increased inter-shelter distances resulted in decreased approaches to resident shelters by intruders. Taken together, these data suggest that increased value of a resource due to quality or availability is the primary driver of population-wide interactions and resource control. As resource values increase, prior contest experience and resource ownership become imperative to obtain and maintain control of a resource and higher dominance rankings that confer fitness advantages.

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**References**


Shelter distribution, social experience influences dominance


