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Fighting Strategies in Crayfish *Orconectes rusticus* (Decapoda, Cambaridae) Differ with Hunger State and the Presence of Food Cues

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Abstract

Crayfish, bearing dangerous weapons in the form of chelae, resolve intraspecific conflicts using stereotyped behaviors and structured, escalated encounters. According to predictions of game theory models, any decision to resort to unrestrained combat without prior careful behavioral assessment of the opponent's fighting abilities carries great risks. The present study examines the significance of internal hunger states and the presence of chemical food cues in this decision process using a 2×2 factorial design. Hungry crayfish escalated more rapidly, and thus took greater risks, during agonistic encounters, while the presence of a food source reduced the rate at which fights increased in intensity. However, there were no significant differences in fighting behavior as a result of the interaction between these two variables. We then address the complex trade-offs that individuals face in fighting with respect to increased risks of injury, appetitive states, and opportunities for resource access.

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Introduction

Animals should be more persistent and willing to take risks in situations where the perceived value of a contested resource is high (Enquist & Leimar 1987; McNamara & Houston 1989). Animals should also employ a risk-prone foraging strategy when they have been deprived of food for an extended length of time (McNamara & Houston 1986; Godin & Crossman 1994). Thus, the significance of a resource depends both on its inherent quality and on the animal's internal state governing its perceived value (McNamara & Houston 1989). Hungry animals

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should thus exhibit a heightened motivational state towards agonism compared to satiated individuals (Wilcox & Ruckdeschel 1982; Lawton 1987; Griffiths 1992). Similarly, individuals may also be more aggressive when an actual food source is present and at stake (DiMarco & Hanlon 1997; Sirot 2000). How such effects influence behavior individually, as well as in the form of interactions between them, has received little attention to date. Crayfish, like most crustaceans, possess remarkable chemosensory systems, allowing them to orient towards a food source (Moore & Grills 1999), locate the desired items (Giri & Dunham 1999), and possibly distinguish between various types of food sources (Hazlett 1994). In the field crustaceans aggregate to food (Barnes 1997) and compete for such items (Jacoby 1982; Sirot 2000). Consequently, resource holding potential (RHP) refers to the individual's ability to attain choice items in the face of competition from conspecific opponents (Parker & Rubenstein 1981). During agonistic encounters individuals match their own strength to that of the opponent, thereby guiding their decisions to escalate, retaliate, or retreat (Beecher 1989). This situation resembles a sequential assessment game, where an agonistic interaction primarily serves to compare increasingly detailed estimates of RHP (Smith et al. 1994) using physical (DiMarco & Hanlon 1997), visual (Bruski & Dunham 1987), chemical (Zulandt-Schneider et al. 1999), or other unexplored senses.

Interactions between closely matched individuals typically escalate over time (DiMarco & Hanlon 1997; Guiasu & Dunham 1997). The risk of injury thereby increases with each step-up in intensity (Cairns & Scholz 1973; Huntingford et al. 1995), particularly without sufficient prior assessment of the opponent. Game theory models of fighting consider the consequences of major decisions, such as whether an animal initiates encounters, continues fighting at the current intensity, escalates to the next higher intensity, retaliates if the opponent escalates, or withdraws from further combat at any given stage in the fight. The particular strategies contestants utilize are sensitive to absolute values, relative differences, and asymmetries in information of a variety of factors. These include: size and physical superiority (Rutherford et al. 1995; Pavey & Fielder 1996; Barki et al. 1997); molt stage (Tamm & Cobb 1978); gender (Sinclair 1977); prior residence (Peeke et al. 1995; Huntingford & deLeaniz 1997); reproductive condition (Debuse et al. 1999); aggressive state (Huber et al. 1997; Huber & Delago 1998); metabolic state (Sneddon et al. 1998); previous agonistic experience (Rubenstein & Hazlett 1974; Gössmann et al. 2000); levels of social isolation (Dunham 1972); and assessment of both the opponent (Archer 1988) and of the resource at stake (Hazlett et al. 1975; Sneddon et al. 1997; Vye et al. 1997).

This study specifically aims to explore variation in fighting strategies of crayfish with respect to differences in hunger states, knowledge about the presence of a food source, as well as an interaction between them. Hungry individuals engage in more fights compared to satiated animals (Hazlett et al. 1975). Despite diminished energy reserves, they must expend more energy at an elevated risk in attempting to acquire the necessary sustenance. With a focus on individual aggressive states and on particular fighting strategies used, a factorial design considers the importance of treatment and interaction effects. We predict that hungry animals will employ more risk-prone aggressive strategies compared to satiated individuals and that the presence of a chemical food cue will result in similar effects.

Methods

Experimental Animals and Laboratory Set-Up

Freshwater crayfish, *O. rusticus*, were collected from the Portage River, 15 miles east of Bowling Green, Ohio, during the months of June and Aug. 1999. Only males of form 1 reproductive state (Turner 1926) at inter-molt (Aiken 1973) with a body mass ranging from 4.1 g to 23.0 g (descriptive statistics listed in Table 1) and with all appendages intact were included. Crayfish were housed individually in containers (Ø = 160 mm) in trays (2.05 m wide × 0.67 m deep at 95 mm water level) equipped with a flow-through system, separating them visually and physically, but not chemically. The water was continuously filtered, aerated, and maintained at 20°C at a constant light regime (16 h light : 8 h dark). All individuals were isolated for 14–17 d, during which the 'satiated' group was fed every 2nd day with pelleted fish food (HBH Enterprises, Provo, Utah) and the 'hungry' group (after an initial feeding) was not fed at all. The experimental chamber (0.55 m wide × 0.25 m deep × 0.13 m water level) was constructed from opaque (white) Plexiglass and with a glass front for viewing. The tank was filled with gravel (7.5 mm deep) and had two holes where water was fed into the tank near the center from a filtered and aerated tub, and two holes near each edge where it drained (this was averted into a drain). A constant flow rate of 1 l/min was maintained.

Table 1: Descriptive statistics for 40 pairs of crayfish used in this study. Displayed in a 2 × 2 factorial matrix are the number of crayfish in each group (n), average body mass, length (mean ± standard deviation) and the degree of size matching (mean percentage ± standard deviation)

	Worms	Water
Satiated		
n	20	20
Mass (g)	10.10 ± 5.29	10.36 ± 4.91
Mass difference (%)	6.19 ± 2.26	4.07 ± 5.33
Length (cm)	2.93 ± 0.40	3.06 ± 0.25
Length difference (%)	1.97 ± 2.21	3.36 ± 2.79
Hungry		
n	20	20
Mass (g)	10.09 ± 4.91	8.60 ± 2.24
Mass difference (%)	6.94 ± 5.15	6.19 ± 1.42
Length (cm)	2.98 ± 0.38	3.01 ± 0.23
Length difference (%)	3.09 ± 2.64	2.31 ± 2.23

Experimental Techniques

Crayfish were assigned randomly to weight-matched pairs (< 15% difference). All individuals were subjected to the same manipulations, and their match was verified by re-weighing them 1 d prior to the scheduled trial. Food-deprived individuals only experienced an average weight loss of 0.048 g (i.e. 0.51% of body weight) during the 2-week period, while fed animals had 0.028 g mean weight gain (i.e. 0.27% of body weight). Individuals were placed into the experimental arena separated by an opaque plastic divider. Following an acclimation period of 5 min the divider was removed and the crayfish were allowed to interact for 30 min. All experiments were carried out between 11:00 and 17:00 h, and were video-taped for subsequent analysis (using either a Sony Digital 8 DCR-TR7000 or Canon XLI Digital Camcorder).

Experiments utilized a 2 × 2 factorial design with hunger state (hungry, satiated; see above) and the chemical cue of a familiar food item (presence, absence) as factors. Manipulations of food cues consisted of the addition of either earthworm homogenate, which is a common natural food source for these wild-caught animals (Momot et al. 1978), at a concentration of 1 g of worm per 20 ml of water (worms), or water alone (control). Upon removal of the opaque divider, an initial 20 ml of worm homogenate was added at the center of the tank, then a further 7.0 ml was added subsequently at 5-min intervals (in the same fashion) to maintain a relative concentration of 1 ml homogenate per 850 ml water. A flow of 1 l/min rapidly dispersed the cloud into a homogenous distribution in 10 s.

Behavioral Analysis

A total of 524 agonistic interactions were characterized in 40 pairs of crayfish with regard to the following characteristics: fight duration; its maximum intensity; rates of escalation; and identities of initiating and retreating individuals. The start of an interaction was defined as the time at which both contestants were within one body length and visibly responded to each other's presence (did not ignore one another). The approaching animal was termed the initiator and the intensity of the initiation was measured on a three-level scale: (i) slow approach (< 1 body length/s); (ii) rapid approach (> 1 body length/s); (iii) lunge. As the interaction progressed, the maximum intensity was determined according to the following five-level scale: 0, at least one individual retreats immediately (no contest); 1, both individuals contest the interaction and at least one shows threat displays and postures without physical contact; 2, both contest and at least one pushes the other without grasping, and or touches it with its antennae; 3, both contest and at least one animal grabs the other with its claws; 4, both contest and at least one exhibits unrestrained use of claws where the animal engages in an apparent attempt to inflict injury on its opponent. The number of times intensity 4 had occurred during the interaction was also noted. The interaction ended when one animal walked or turned away, increasing the distance between them to more than one body length for at least 5 s. Retreat was measured on a three-level scale: 1, slow retreat ($<$ 1 body length/s); 2, fast retreat ($>$ 1 body length/s); and 3, tail-flip. This approach relies on the characterization of well-defined behavioral parameters which can be assessed consistently by different observers. Methods have been validated repeatedly and inter-observer reliability is high. Additional detail about these techniques underlying our measures of fighting behavior have been outlined elsewhere (Huber et al. 2001).

Statistical Evaluation

The effects of both factors, hunger state and presence of food cues by themselves, as well as their interaction effects were estimated using two-way analysis of variance (ANOVA) in the case of continuous variables (e.g. fight duration) and analysis of log-likelihood for ordinal variables (e.g. maximum intensity). A best-fit regression line (regression plot) was used to explore the relationship between fight duration (i.e. the rate of escalation) and its maximum level of intensity. A linear ANOVA was used to statistically compare differences in slope. All analyses were performed with JMP 3.2.2 (SAS Institute, 1997) with significance set at $p < 0.05$.

Results

The intensity and number of fight initiations were consistently higher in the presence of worm homogenate (Fig. 1). However, there were no significant

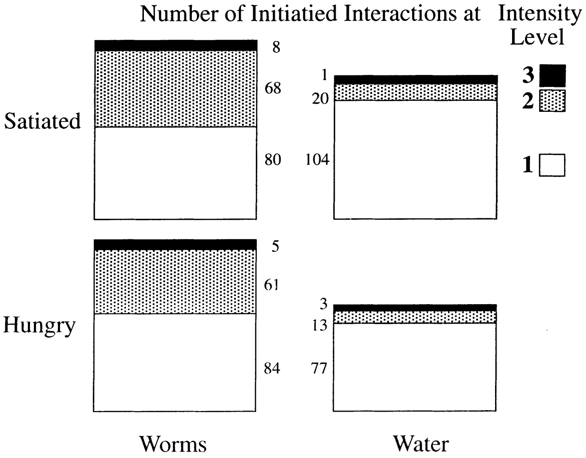

Fig. 1: Initiation intensity is plotted as a collection of stacked bar graphs in 2 × 2 factorial matrices showing the overall number of fights in each treatment as well as the relative number of fights that reached each intensity level. Initiation intensity differed between food cue ($\chi^2_{[1]} = 16.42$, $p < 0.001$) but not between hunger treatments ($\chi^2_{[1]} = 0.03$, $p = 0.873$) or the interaction (not visually depicted) between the two variables ($\chi^2_{[1]} = 0.38$, $p = 0.536$)

differences in these variables between hungry and satiated animals or as a function of the interaction between these two variables (Fig. 1). Neither hunger state nor the presence of food cues or their interaction effects explained differences in fight duration (hunger: $F_{[1,520]} = 0.51$, $p = 0.48$; food cue: $F_{[1,520]} = 2.04$, $p = 0.15$; interaction: $F_{[1,520]} = 1.11$, $p = 0.29$), the number of times intensity 4 was reached (hunger: $F_{[1,15]} = 0.68$, $p = 0.42$; food cue: $F_{[1,15]} = 0.15$, $p = 0.71$; interaction: $F_{[1,15]} = 0.10$, $p = 0.76$) or in maximum intensity (hunger: $\chi^2_{[1]} = 0.06$, $p = 0.81$; food cue: $\chi^2_{[1]} = 0.48$, $p = 0.49$; interaction: $\chi^2_{[1]} = 2.38$, $p = 0.12$). Rates of escalation varied between hunger states and the presence/absence of food. A significant best-fit regression line demonstrated that the duration of each interaction effectively explained its maximum intensity (Fig. 2) in every treatment group and thus provided a valid estimate for the rate at which intensities increased during the encounter. Encounters escalated more rapidly (i.e. the slope of the regression line was steeper) in pairs of hungry individuals compared to satiated animals (Fig. 2). Moreover, fights escalated more slowly in the presence of food and there were no significant interaction effects between these variables (Table 2). Finally, the intensity at which animals retreated was affected neither by the treatments alone (hunger: $\chi^2_{[1]} = 0.09$, $p = 0.93$; food cue: $\chi^2_{[1]} = 0.94$, $p = 0.33$) nor by their interaction ($\chi^2_{[1]} = 3.80$, $p = 0.06$).

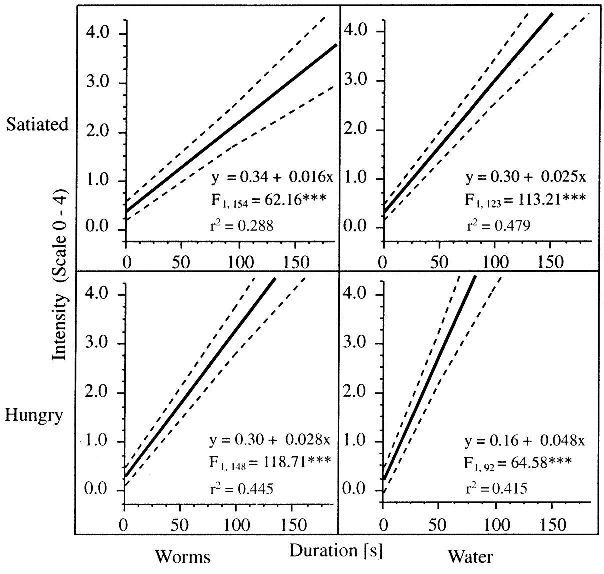

Fig. 2: The rate of escalation is displayed in a 2 × 2 factorial matrix. The regression line equation is: maximum intensity y = intercept + (rate of escalation × fight duration). Escalation rates differ between hunger treatments ($F_{[1,\ 516]} = 12.020$, $p < 0.001$) and between food cue preparations ($F_{[1,\ 516]} = 9.114$, $p = 0.003$). Individual F-values for the regression lines and r^2-values are contained within the figure ($p < < 0.001$***)

Table 2: The factorial source table for the rate of escalation. The effect of each term measured on maximum intensity as well as the interaction of those effects are depicted

Source	df	SS	MS	F	p
Duration	1	62.567	62.567	64.490	< 0.001
Hunger State	1	0.858	0.858	0.883	0.348
Food Cue	1	0.888	0.888	0.915	0.339
Hunger × food cue	1	0.296	0.296	0.305	0.581
Duration × hunger	1	11.661	11.661	12.020	< 0.001
Duration × food cue	1	8.842	8.842	9.114	0.003
Duration × hunger × food cue	1	2.226	2.226	2.294	0.131
Error	516	500.602	0.970		
Total	523	836.359			

Discussion

The present study demonstrates that choices with regard to fighting strategies are contingent on both internal state as well as the perceived presence of a resource. In the presence of chemical food cues, crayfish initiated encounters with increased intensity compared to controls. To a large extent, the probability of fight initiation is contingent on the extent of locomotor activity (Huber & Delago 1998). Chemical food cues, which increase walking speed (Steele et al. 1999), thus also automatically lead to a rise in the number of interactions. A heightened aggressive state was indicated by a parallel increase in the intensity at which fights were initiated.

Hungry crayfish escalated fights more rapidly than satiated individuals, while chemical food cue controls were higher compared to worm manipulations (Fig. 2). The opportunities for future resource utilization ought to determine which particular strategies are used (Enquist & Leimar 1990). Hungry individuals may have ‘less to lose’ because food deprivation reduces chances for survival (McNamara & Houston 1989), and thus adopt more dangerous fight strategies. Alternatively, hungry crayfish may place increased value on time spent fighting because this takes away from opportunities to forage (Griffiths 1992).

Fighting in the presence of food cues lasted longer compared to controls. Extended interactions at a constant rate of escalation are generally thought to occur in such an instance due to a decrease in the probability for retreat (Smith et al. 1994). Consistent with this idea, fighting tended to be of longer duration in situations that involved increased resource value (Enquist et al. 1998). Other empirical evidence contradicts this prediction, where the presence of a valued resource generally fosters conditions for fights that are shorter and escalate more rapidly (Riechert 1979; Caldwell 1987; DiMarco & Hanlon 1997; Sneddon et al. 1997). Present experiments did not control for relative resource value to each participant (Enquist & Leimar 1987). In the case of asymmetries, fights ought to be resolved faster and animals should be more likely to take risks (Parker & Rubenstein 1981; Enquist & Leimar 1987). In the current study, the presence of food odor suggests the availability of edibles nearby. A decrease in most measures of fighting may thus indicate a trade-off between interests in exploring the vicinity and engaging the opponent. Food cues may thus act as a distraction.

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