Aquat Ecol (2020) 54:889–894
https://doi.org/10.1007/s10452-020-09775-9

The effects of satiation level and competition risk on resource acquisition in red swamp crayfish (*Procambarus clarkii*)

Ciara J. Mergler · Alexandra N. Ludwig · Brian G. Gall

Received: 19 March 2020 / Accepted: 21 May 2020 / Published online: 30 May 2020

Abstract Strategies of resource acquisition are subject to change due to introduced pressures placed upon individual animals. The pressures of food deprivation and competition can lead to a drastic change in previously established strategies of resource acquisition. We conducted a series of trials in which red swamp crayfish (*Procambarus clarkii*) were either deprived of food or satiated and competition was introduced via a plastic model to necessitate the abandonment of established resource acquisition strategies in favor of risk-insensitive strategies. Crayfish exhibited no difference in behavior when exposed to a singular pressure; however, an interaction between food deprivation and competition was detected and indicates that crayfish responded to food sources more quickly and with more risk-insensitive behavior when a model competitor was present. This combination of factors indicates a complex relationship between resource acquisition strategies and the pressures of acquiring food.

Keywords Hunger · Model · Exploitation · Interference

Handling Editor: Télesphore Sime-Ngando.

C. J. Mergler · A. N. Ludwig · B. G. Gall (✉)
Department of Biology, Hanover College, 517 Ball Drive,
Hanover, IN 47243, USA
e-mail: gall@hanover.edu

Introduction

Resource acquisition is the most fundamental necessity for the survival of an individual, the intense pressure of which ultimately leads to the formation of highly evolved and specialized strategies (Baird 1991; Milinski 1982). These strategies can be employed in foraging and agonistic behaviors and are subject to the influence of multiple factors. One of the most studied interactions is the association between food deprivation and both risk-prone behavior and agonistic encounters (Adlerstein and Fehrer 1955; Barnard and Brown 1985; Bateson 2002; Hazlett et al. 1975; Stocker and Huber 2001). Previous studies have demonstrated how the survival pressure introduced by food deprivation results in more risk-insensitive and aggressive behaviors when faced with the payout of potential food. In this case, the introduced factor of food deprivation necessitates a trade-off in strategies, in which animals sacrifice risk-aversion for the sake of obtaining limited resources.

One of the most common occurrences in which animals must sacrifice risk-aversion is in the face of competition. There are multiple variables that determine how organisms react when faced with competition. For example, there are extrinsic factors, such as resource availability and shelter presence, that affect the severity and type of competition that an organism will display (Bergman and Moore 2003). The severity of competition is especially heightened when the resource is of limited supply (Bovbjerg 1953; Bruski and Dunham 1987; Hazlett et al. 1975; Pintor et al. 2008). A resource that is limited to patches, for instance, may force individuals to congregate together and instigate interference competition including physical fighting and intimidation (Schoener 1983; Pintor 2007; Bergman and Moore 2003). There are also intrinsic factors, such as body size, sex and hunger state, that affect the behavior of individuals (Bergman and Moore 2003). For example, organisms that have been food-deprived have been shown to increase locomotion and foraging behavior (Capelli and Munjal 1982; Stocker and Huber 2001; Hazlett et al. 1975). In this scenario, individuals employing exploitative competition deprive others of the resource by getting to the resource more quickly (Schoener 1983). However, deviations from this expected outcome are likely to occur in the field where both competition and food deprivation combine to govern animal behavior.

North American crayfish have been extensively used in studies on the effects of food deprivation on risk and agonistic behaviors. These crustaceans are ideal candidates for such study as they are known for having a highly predictable and regimented hierarchical rank under standard laboratory conditions (Bovbjerg 1953; Capelli and Munjal 1982; Goessmann et al. 2000; Stocker and Huber 2001). Crayfish dominance is generally correlated with body size whereby larger crayfish are more likely to exhibit dominant and aggressive behavior in comparison with those that are smaller (Bovbjerg 1953, 1956; Capelli and Munjal 1982; Goessmann et al. 2000; Pavey and Fielder 1996). Likewise, crayfish are reliably and predictably more aggressive after periods of food deprivation (Hazlett et al. 1975; Hazlett 2003; Stocker and Huber 2001). The confluence of these two factors—an established hierarchy dictating agonistic encounters and the heightened aggression in response to deprivation—creates a scenario in which typically reliable responses to food acquisition may become unpredictable. For example, when animals are faced with the risks of starvation vs. the risks of heightened competition, they may be willing to sacrifice risk-aversion in order to obtain some benefit (Barnard and Brown 1985; Milinski 1982; Svanback and Bolnick 2005).

Given the potential trade-off organisms face between food acquisition and competition in the wild, we conducted a study to evaluate the combination of these factors in red swamp crayfish (*Procambarus clarkii*). Specifically, crayfish were reared under food-deprived or satiated conditions. These individuals were then fed in the presence or absence of a model competitor exhibiting an agonistic posture. We hypothesized that hunger state would shift the risk-averse behavior of crayfish when in the presence of an agonistic model.

Methods

Animal maintenance

Red swamp crayfish (*Procambarus clarkii*) were purchased from a commercial supplier (Carolina Biological Supply Company) in November 2019. Crayfish ranged in size from approximately 4–8 cm and were left unsexed. Crayfish were housed individually in plastic containers of varying size (approximately 3 L). Containers were filled with dechlorinated water to a depth of approximately 15 cm. Water changes within the tanks were performed every 2–3 days. Each crayfish was provided a shelter consisting of ceramic tile and plastic tubing. Containers were housed in an environmental chamber where they were maintained at 20 °C on a 12-h-day/night light cycle. All crayfish were fed a daily mixture of chicken liver (*Gallus gallus*) and crayfish food pellets (Carolina Biological Supply Company) for 6 days; enough food was provided to satiate crayfish and excess food or waste was removed 3–5 h post-feeding. One week prior to experimentation, half of the crayfish ($n = 37$) were randomly selected and were deprived of food. The remaining crayfish ($n = 31$) were held on the normal feeding schedule as described above to ensure satiation.

Experimental design

Experimental trials were conducted within each crayfish's home container. For each trial, a crayfish that was satiated or food-deprived was selected and was randomly assigned to either the control treatment or the experimental treatment. The container lid and shelter were removed. A five-minute acclimation period was then initiated. In the control treatment, a piece of chicken (*Gallus gallus*) liver (∼ 2 cm) was deposited into the container approximately 8 cm away from the crayfish. Care was taken to deposit the liver with as little disturbance to the water as possible, so as to minimize disruption to the test animal. Experimental treatments likewise received a piece of liver; however, in this treatment, a model crayfish was placed in the tank immediately after liver was introduced. The model crayfish were 6.35-cm soft plastic fishing lures (Yum CrawBug) glued to a glass rod. The model was structurally fortified by embedding thin wire through the body and chelae. The model's chelae were positioned so that they were extended upwards and laterally away from the body in a meral spread, the crayfish's defensive and offensive posture (Bovbjerg 1953, 1970; Bruski and Dunham 1987). The model was positioned next to the liver with one claw in contact with the food. Following the introduction of either food or food and a model, a 60-min observation period then commenced. During this observation period, the latency to eat and any displays of aggression or retreat were recorded. Eating behavior was recorded only once the crayfish manipulated the liver and began to consume it. Aggressive behaviors were determined by either passive displays such as a meral spread of the chelae or by active manipulation of the model, including any sort of pinching or striking. Retreat behaviors were recorded when the crayfish orientated toward the model and then fled from the model, most often through the use of a tail flip or slowly walking backwards. Once the crayfish began to consume the liver, the trial was concluded; if the crayfish did not respond to food within an hour, their latency was recorded as 3600 s. The model crayfish were rinsed with tap water between each use.

Statistical analysis

We compared the latency to eat between crayfish using a two-way ANOVA with food treatment (satiated vs. deprived) and model presence (present vs. absent) as the two main effect factors. When a significant interaction term was identified, Tukey's post-hoc comparisons were conducted. Sigmaplot v. 12.5 was used for all analyses. Assumptions of normality and homoscedasticity were met by these data.

Results

Out of 68 total trials, 35 crayfish consumed the food. Of these, the majority ($n = 27$) belonged to the group that had been deprived of food. Of the crayfish which had been satiated prior to experimentation, only 23% consumed food; crayfish from the deprived treatment had a consumption percentage of 73%. A two-way ANOVA indicated that there was no significant effect of the model presence on the latency to eat ($F_{[1, 64]} = 1.1$, $P = 0.3$). However, we found a significant main effect of hunger level on the latency to eat ($F_{[1, 64]} = 23.3$, $P < 0.001$) and a significant interaction between food level (satiation vs. deprivation) and model presence (absent vs. present) on the latency to eat ($F_{[1, 64]} = 5.552$, $P = 0.022$, Fig. 1). In this case, satiated crayfish responded with a similar latency to eat regardless of the presence or absence of the model ($P = 0.374$, Fig. 1). However, the crayfish which had been deprived of food prior to trials demonstrated a significantly lower latency to eat in response to the presence of a model ($P = 0.015$, Fig. 1). Post-hoc comparisons indicated that when the model was present, deprived crayfish showed a significantly lower latency to eat in comparison with satiated crayfish ($P < 0.001$, Fig. 1). However, satiated and

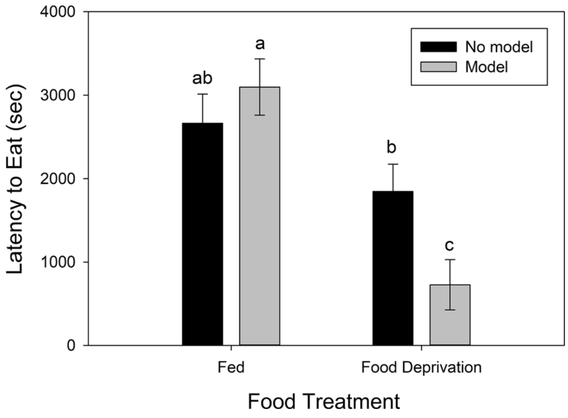

Fig. 1 Mean (± SE) latency for satiated and food-deprived crayfish (*Procambarus clarkii*) to eat with a model crayfish either present or absent. A significant interaction between satiation level and model presence indicates that crayfish deprived of food responded to the model differently than satiated crayfish ($F_{[1, 64]} = 5.552$, $P = 0.022$). Deprived crayfish reduced their latency to eat in response to the model being present, whereas satiated crayfish responded the same regardless of the model's presence or absence. Different letters indicate a significant difference between treatments ($P < 0.05$)

food-deprived crayfish did not respond differently to the presence of food without a model ($P = 0.093$, Fig. 1).

Discussion

Previous studies have demonstrated how food deprivation leads to an increase in foraging, exploratory and agonistic behaviors (Adlerstein and Fehrer 1955; Day et al. 1995; Hazlett et al. 1975; Stocker and Huber 2001). Several previous studies have been conducted on crayfish to investigate the influence of satiation level and food presence on aggression. However, these studies have not included the presence of a competitor, and as such could not compare how the presence or absence of competition affects responses to provided food (Hazlett et al. 1975; Stocker and Huber 2001). The results of this study indicate a more complex relationship between food deprivation, competition and subsequent foraging behavior. In trials where no model was present, both satiated and deprived crayfish responded similarly to the provided food. Regardless of satiation or deprivation, these animals were equally slow to respond to the food and over half (56%) did not consume anything during the observational period, including those that had been deprived of food. Only when the model crayfish was placed in the experimental chamber did a significant shift in behavior within the food-deprived group occur. In this case, the inclusion of the model spurred the live crayfish to consume the provided food more quickly in comparison with the crayfish who were not exposed to a model. Since food is a limited resource that is valuable and defendable, it should act to increase interference competition when in short supply (Dingle 1983; Barki et al. 1997; Hazlett et al. 1975). This increase in competition would take time from foraging and ultimately lead to a delay in the acquisition of food (Martin and Corkum 1994). By combining the influences of food supply and competition, we predicted that deprived crayfish would take more time to directly compete with a model over food and thus be delayed in acquiring resources as compared to other deprived crayfish with no competing model. However, our results indicated that food-deprived crayfish presented with a model took less time to eat than food-deprived crayfish without a model. The model crayfish likely acted as a source of artificial competition for the limited resource, thus introducing a secondary motivation for risk-indifferent food acquisition, which animals are known to face more willingly after periods of food deprivation (Bateson 2002; Cabanac and Johnson 1983; Charnov 1976).

These results can likely be explained by the crayfish's well-documented tendency toward increased aggression in response to food deprivation. Previous trials have examined levels of aggression and the potential for agonistic interactions between crayfish following periods of food deprivation. All such studies have demonstrated an increase in agonistic behaviors, especially when provided with an extra incentive of food acquisition (Capelli and Munjal 1982; Hazlett et al. 1975; Hazlett 2003; Stocker and Huber 2001). Our results also indicate a similar trend in which crayfish which were deprived of food demonstrate a higher likelihood of actively manipulating and interacting with the model (47% within the deprived group vs. 25% within the satiated group). Within the satiated group, the only crayfish to consume food were the individuals which interacted with the model; the remaining satiated crayfish did not interact with the model or food.

Size and sex are important in determining whether crayfish will display aggressive behavior and win potential contests. For example, multiple size classes of crayfish may be present in a population at one time, and older and larger individuals generally outcompete younger age-classes (Bovbjerg 1953). Similarly, males generally outcompete females within the same age class, and individuals of the same age and sex even form distinct dominance hierarchies (Bovbjerg 1953, 1956; Goessmann et al. 2000). With the difference in dominance according to size, the expected response would be for the crayfish larger than the model to exhibit a stronger inclination toward aggression and those smaller than the model should hesitate to interact. Body size of the crayfish was not recorded in this study, yet anecdotal observations during experimental trials suggest that this is not the case. Crayfish which were smaller than the model appeared to interact with and manipulate the model just as readily as larger crayfish. Because our experiment used models that were immobile instead of live crayfish, and thus made no aggressive advances, our crayfish may have implemented exploitative competition according to the passive behavior of the competitor (Pintor and Sih 2009). Regardless, further studies that evaluate this interaction while also factoring in crayfish size, sex and developmental age (e.g., juvenile vs adult) are necessary to fully elucidate how food deprivation and competition interact to influence crayfish behavior. In addition, the use of an inert model eliminated the role of chemical information in these trials. Chemical information is critical to the assessment of predator–prey interactions, mating and competition in aquatic settings (Bronmark and Hansson 2000) and is used extensively by crayfish (Moore and Bergman 2005; Breithaupt 2010). Future work incorporating the role of chemical cues to understand the relationship between the variables assessed in this study is warranted.

Previous studies have indicated that crayfish respond to periods of food deprivation with an increase in aggression levels. While our study supports this notion, our results indicate a more complex interaction between factors leading to crayfish aggression and risk-prone food acquisition. Food deprivation alone did not lead to any indication of increased agonistic behavior or decreased latency to eat. Only with the confluence of food deprivation and the additional influence of introduced competition do crayfish exhibit a distinct difference in their strategies toward food acquisition and potential competitors. Further testing that combines additional measures, such as the body size of the crayfish compared to the competitor, number of competitive behaviors and total time spent consuming the food, would increase the durability of these results.

Acknowledgements This research was funded by the Hanover College Department of Biology, without which such trials would not have been possible. We thank Lisa Quiroga and Ariel Barlow for their assistance and contribution to these trials. We also extend our gratitude to our advising professor for providing his expertise and long-suffering patience during the tribulations of this experiment. A special thank you goes out to our friends Summer Brown and Emilee Greathouse who were unwittingly, yet graciously, coerced into assisting in the maintenance and care of crayfish. This paper is written in commemoration of Zombie, the little crayfish which seemingly returned from the dead no less than three times.

References

Adlerstein A, Fehrer E (1955) The effect of food deprivation on exploratory behavior in a complex maze. J Comp Physiol Psychol 48:193–206

Baird PH (1991) Optimal foraging and intraspecific competition in the Tufted Puffin. The Condor 93:503–515

Barki A, Sheenan H, Karplus I (1997) Contradictory asymmetries in body and weapon size, and assessment in fighting male prawns, Macrobrachium rosenbergii. Aggress Behav: Off J Int Soc Res Aggress 23:81–91

Barnard CJ, Brown CA (1985) Competition affects risk-sensitivity in foraging shrews. Behav Ecol Sociobiol 16:379–382

Bateson M (2002) Recent advances in our understanding of risk-sensitive foraging preferences. Proc Nutr Soc 61:509–516

Bergman DA, Moore PA (2003) Field observations of intraspecific agonistic behavior of two crayfish species, *Orconectes rusticus* and *Orconectes virilis*, in different habitats. Biol Bull 205:26–35

Breithaupt T (2010) Chemical communication in crayfish. In: Breithaupt T, Martin T (eds) Chemical communication in crustaceans. Springer, Berlin, pp 257–276

Bovbjerg RV (1953) Dominance order in the crayfish *Orconectes virilis* (Hagen). Physiol Zool 26:173–178

Bovbjerg RV (1956) Some factors affecting aggressive behavior in crayfish. Physiol Zool 29:127–136

Bovbjerg RV (1970) Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilus* and *Orconectes immunis*). Ecology 51:225–236

Bronmark C, Hansson L (2000) Chemical communication in aquatic systems: an introduction. Oikos 88:103–109

Bruski CA, Dunham DW (1987) The importance of vision in agonistic communication of the Crayfish *Orconectes rusticus*. I: An analysis of bout dynamics. Behaviour 103:83–107

Cabanac M, Johnson KG (1983) Analysis of a conflict between palatability and cold exposure in rats. Physiol Behav 31:249–253

Capelli GM, Munjal BL (1982) Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. J Crustac Biol 2:486–492

Charnov EL (1976) Optimal foraging, the marginal value theorem. Theor Popul Biol 9:129–136

Day JE, Kyriazakis I, Lawrence AB (1995) The effect of food deprivation on the expression of foraging and exploratory behavior in the growing pig. Appl Anim Behav Sci 42:193–206

Dingle H (1983) Strategies of agonistic behavior in Crustacea. In: Rebach S, Dunham DW (eds) Studies in adaptation: the behaviour of higher Crustacea. Wiley, New York, pp 85–111

Goessmann C, Hemelrijk C, Huber R (2000) The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. Behav Ecol Sociobiol 48:418–428

Hazlett B (2003) The effects of starvation on crayfish responses to alarm odor. Ethology 109:587–592

Hazlett B, Rubenstein D, Rittschof D (1975) Starvation, energy reserves, and aggression in the crayfish *Orconectes virilis* (Hagen, 1870) (Decapoda, Cambaridae). Crustaceana 1:11–16

Martin GW, Corkum LD (1994) Predation of zebra mussels by crayfish. Canad J Zool 72:1867–1871

Milinski M (1982) Optimal foraging: the influence of intraspecific competition on diet selection. Behav Ecol Sociobiol 11:109–115

Moore PA, Bergman DA (2005) The smell of success and failure: the role of intrinsic and extrinsic chemical signals on the social behavior of crayfish. Integr Comp Biol 45:650–657

Pavey CR, Fielder DR (1996) The influence of size differential on agonistic behaviour in the freshwater crayfish, *Cherax cuspidatus* (Decapoda: Parastacidae). J Zool 238:445–457

Pintor LM (2007) The influence of invader traits and community characteristics on the invasion success of an exotic crayfish. Dissertation, University of California Davis

Pintor LM, Sih A, Bauer ML (2008) Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. Oikos 117:1629–1636

Pintor LM, Sih A (2009) Differences in growth and foraging behavior of native and introduced populations of an invasive crayfish. Biol Invasions 11:1895–1902

Schoener TW (1983) Field experiments on interspecific competition. Am Nat 122:240–285

Stocker AM, Huber R (2001) Fighting strategies in crayfish *Oronectes rusticus* (Decapoda, Cambaridae) differ with hunger state and the presence of food cues. Ethology 107:727–736

Svanback R, Bolnick DI (2005) Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. Evol Ecol Res 7:993–1012

Tierney AJ, Godleski MS, Massanari JR (2000) Comparative analysis of agonistic behavior in four crayfish species. J Crustaceans Biol 20:54–66