J Ethol (2004) 22:23–27
DOI 10.1007/s10164-003-0095-x

ARTICLE

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Habitat complexity reduces aggression and enhances consumption in crayfish

Received: January 21, 2002 / Accepted: August 5, 2002 / Published online: February 13, 2003

Abstract We tested the hypothesis that increased habitat complexity would reduce intraspecific interactions among crayfish (*Orconectes propinquus*), and result in an increase in the consumption rate of prey at different crayfish densities. The effect of crayfish density, food level (trout eggs), and habitat complexity on prey consumption by crayfish was quantified in the laboratory. There was a significant difference in the consumption rate between different food levels. When food was scarce, almost all trout eggs were consumed regardless of crayfish density or habitat complexity. When food was unlimited, there was a significant positive linear relationship between eggs consumed per crayfish and habitat complexity. However, the relationship was not significant when trials without habitat were deleted from the analysis. We found that habitat complexity significantly reduced intraspecific aggression. Our findings suggest that a minimal amount of habitat complexity can reduce interactions among predators, ultimately resulting in increased prey consumption.

Key words Density · Habitat · Interactions · *Orconectes propinquus* · Prey consumption

Introduction

Habitat complexity may affect behaviours of predators and prey by altering foraging modes and encounter rates among organisms (Savino and Stein 1982, 1989). Foraging efficiency of predators generally declines with increasing structural complexity due to reduced visual or tactile cues among predators, making it difficult for predators to find prey (Savino and Stein 1982; Gotceitas and Colgan 1989). Thus, complex habitats reduce predation rates by providing hiding places for prey, thereby reducing encounter rates (Anderson 1984; Christensen and Persson 1993).

We argue that increased habitat complexity benefits predators rather than prey if the heterogeneity of the environment reduces interactions among predators, resulting in increased prey consumption. Martin and Corkum (1994) showed a decrease in the per capita rate of mussel (*Dreissena polymorpha*) consumption in simple habitats at elevated crayfish densities (beyond 4 individuals/m^2). Martin and Corkum (1994) speculated that when crayfish density was high, each crayfish ate fewer zebra mussels because the crayfish spent more time fighting with one another. Earlier, Bovbjerg (1959) showed that the number of contacts (avoiding, threatening, striking, fighting) among crayfish (*Cambarus alleni*) was highest at high densities. Surprisingly, few studies examine habitat complexity and foraging among predators (Basquill and Grant 1998).

In this study, we investigate the change in aggression among predators with increasing habitat complexity and examine these effects on the outcome of predator-prey relations. This approach differs from other studies where the focus tends to be on factors that affect the behaviour of the predator alone rather than on the behaviour of the predator and its effect on predator-prey interactions.

We hypothesized that as habitat complexity increases, interactions among crayfish should decrease, resulting in an increase in the amount of food eaten per crayfish. If food is abundant, we anticipated that patterns of prey consumption would be a function of both crayfish density and habitat complexity.

Materials and methods

Orconectes propinquus were collected (12 and 26 July and 6 August 1996) in the Maitland River (near Brussels, Ontario; 81°14′58″, 43°44′42″) using hand-held dip nets. Crayfish were collected in a still water area (10 × 15 m) over substrates of gravel, cobble and small boulders in water depths of 0.25–0.5 m. Crayfish of a similar size (carapace

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length was 2.5–3.0 cm measured using digital calipers) were used for laboratory experiments. Before experiments, crayfish were held in plastic wading pools (0.7 m^2) that contained aerated dechlorinated water, a refuge for each crayfish, and an unlimited supply of shrimp pellets. The light regime was 14 h L:10 h D. Intermolt crayfish were used only once. After experiments, crayfish were returned to the river within 2 weeks of capture and released.

We quantified how limited and unlimited prey (rainbow trout, *Oncorhynchus mykiss*, eggs obtained from a fish hatchery), crayfish density, and habitat complexity influenced prey consumption by crayfish. The design [2 prey levels (3 and 24 rainbow trout eggs per crayfish per day) × 3 levels of increasing crayfish density (2, 4, 8 crayfish per pool) × 5 levels of increasing complexity (0, 2, 4, 6, 8 clay flower pots)] was replicated 3 times ($n = 90$ trials). The crayfish density corresponded to 2.9, 5.7, and 11.5 crayfish per m^2. The maximum density of *Orconectes propinquus* corresponded to the mean density (11.7 ± 5.33 individuals per m^2) in the Maitland River that we had estimated using quadrats. This field site had the highest crayfish density of any other location in the Maitland River drainage basin (basin area: 2,541 km^2, channel length: 145 km). These values were within the range of field densities of *O. propinquus* reported by Momot et al. (1978) at another location of high abundance.

We set up 15 pools (bottom diameter: 94 cm; height: 20 cm) with dechlorinated water that had been aerated for 24 h. The pools were lined with washed gravel (diameter 1.5–5.5 cm) to mimic natural conditions. Water depth in each pool was 15 cm. Eggs were placed in the centre of each pool. Treatments were randomly selected within each replicate and each trial lasted 24 h.

Rainbow trout eggs were used in the experiment because they represented a prey that crayfish readily consume (Savino and Miller 1991). A pilot study was conducted to determine the quantity of eggs to be used in limited and unlimited food treatments. Ten randomly selected crayfish were placed in separate 40-L aquaria (water temperature: ca. 21°C) and deprived of food for 48 h. After fasting, an unlimited supply of eggs were placed into each aquarium. Mean (±SE) consumption of trout eggs by crayfish was 15.4 ± 4.7 eggs per individual after 24 h. On the basis of these findings, we selected limited (3 eggs per crayfish per day) and unlimited (24 eggs per crayfish per day) food levels for the experiment.

Prior to the experiment, crayfish were transferred from their initial holding pools into a second pool where they were deprived of food for 48 h. At the beginning of each experiment, individual crayfish were positioned in designated pools with a refuge set equidistant around the perimeter of a pool such that all crayfish were an equal distance from both food and one another. To determine if crayfish exhibited any fidelity to their original shelter, each crayfish was marked with a number on its carapace using white Liquid Paper, which corresponded to its initial shelter.

Inverted clay flower pots (internal diameter 10 cm, height 10.5 cm) were used to mimic cobbles and to alter habitat complexity in each pool. The placement of each pot was randomly assigned to 1 of 32 locations within each pool. Water temperature in pools was 19–23°C, which was within the daily temperature range of the Maitland River.

Identifying eggs eaten by crayfish was impossible because of their rapid mechanical breakdown in the grinding stomach (Savino and Miller 1991). Thus, we relied solely on the recovery of eggs in the pools to determine prey consumption. After each trial, eggs remaining (if any) in the pool were removed and counted. Gravel and clay pots were examined and removed to ensure that all eggs were retrieved. The pools were then drained and washed.

Multiple regression (General Linear Model; SAS Institute 1985) was used to determine if there were significant associations between the prey consumed and habitat complexity, crayfish density, food levels and their interactions. The null hypothesis was that prey consumption was independent of habitat complexity, crayfish density, and food level. Because we expected that prey consumption would decline with increasing habitat complexity, increasing density, and more food, we used one-tailed tests for significance of these factors.

We also evaluated if contacts among crayfish were associated with degree of habitat complexity (0, 2, 4, 6, 8 clay pots) for the selected treatment of high density and unlimited food that was placed in the centre of the pool. The high density treatment was evaluated because Bovbjerg (1959) had shown that the number of contacts among crayfish was highest at high densities. A Panasonic WV 1260 high resolution infrared video camera and a Panasonic AG6050 time-lapse video recorder monitored crayfish interactions for 24 h.

Results

Prey consumption

There were significant differences in the proportion of prey consumed by crayfish depending on the number of available eggs ($F_{1,82} = 42.16$, $P = 0.0001$; Fig. 1). Also, significant interactions occurred between habitat complexity and food levels ($F_{1,82} = 9.25$, $P = 0.0032$; Fig. 1) and among crayfish density, habitat complexity, and food levels ($F_{1,82} = 3.97$, $P = 0.0495$), which also accounted for the amount of prey consumed by crayfish. When food was scarce, all or almost all of the trout eggs were consumed regardless of crayfish density or habitat complexity (Fig. 1).

When food was unlimited, there was a positive linear relationship between eggs consumed per crayfish and habitat complexity ($Y = 9.67 + 0.44X$, $R^2 = 0.09$, $P = 0.02$, $n = 45$; Fig. 1). However, if data for no habitat complexity were deleted from the analysis, we found that the slope of the regression line between habitat complexity (range 2–8) and trout eggs consumed per crayfish did not differ significantly from zero ($R^2 = 0.015$, $P = 0.12$) when food was unlimited.

Crayfish density also affected prey consumption in cases when food was unlimited (Fig. 2). There were significant positive relationships between prey consumption and habi-

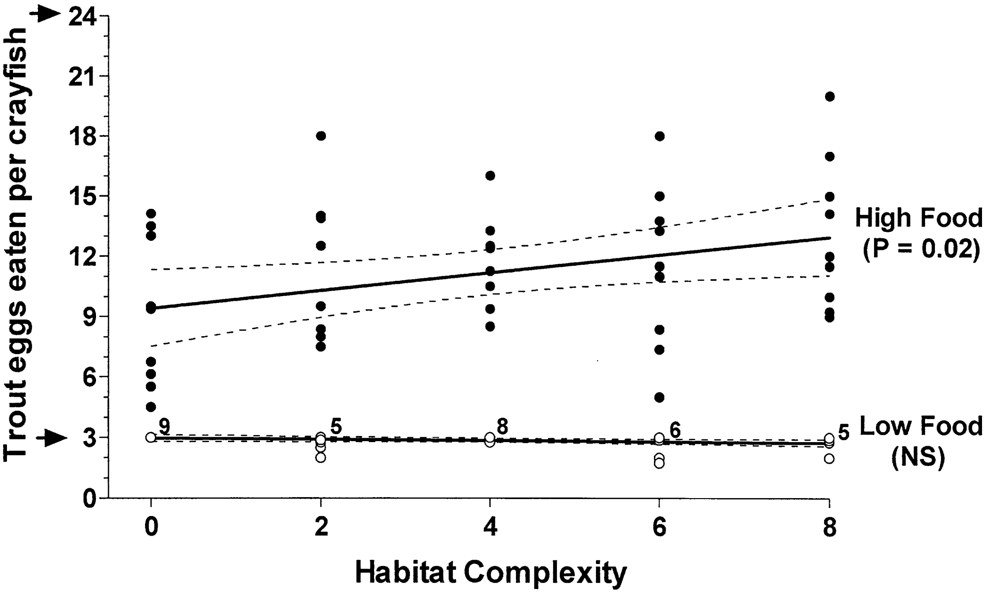

Fig. 1. Relationship between total trout eggs eaten per crayfish and habitat complexity at high and low food levels. *Arrows* at 24 and 3 on the *Y-axis* represent the maximum number of trout eggs available per crayfish at each food level. *Numbers* associated with *symbols* at low food treatments represent the number of cases in which crayfish ate the maximum number of trout eggs. A *regression line* with 95% confidence interval is included

tat complexity at low ($P = 0.031$ when one outlier was deleted) and medium ($P = 0.033$) crayfish densities, but not at high ($P = 0.496$) crayfish density (Fig. 2).

Interactions among crayfish

Crayfish interactions decreased with time such that most activity occurred during the first 12 h. We analysed three randomly selected 10-min segments of videotape for each level of habitat complexity during this active period for the highest crayfish density and unlimited food conditions. Results showed a negative association between number of crayfish contacts and habitat complexity ($Y = 60–4.88X$, $R^2 = 0.36$, $P = 0.009$, $n = 15$; Fig. 3).

Most interactions among crayfish occurred in the centre of the pool, near the feeding area. Repeated matches between the same two crayfish in a given trial were common. Typically, interactions between crayfish were head to head in quick succession with chelae waving. Occasionally a third crayfish would join the interaction and use a chela to hit the body of another crayfish. In matches between two crayfish, chelae struck the head (most common) or body of the opposing crayfish. After bouts of activity, one crayfish would chase the other across the pool. At the end of the 24-h trials, crayfish did not display any homing behaviour as they were seldom found in their initial shelter in which they were placed at the beginning of the experiment.

Discussion

In our study, consumption of rainbow trout eggs by crayfish depended on several factors including crayfish density, food levels and habitat complexity. Of these factors, crayfish consumption of prey depended primarily on the amount of available food. All or almost all food was consumed when resources were scarce, indicating that crayfish may risk interactions with other crayfish to forage when food resources are low. Alternatively, crayfish may fight less when food is limited to conserve energy. When food resources were high, rainbow trout eggs consumed per crayfish and habitat complexity were positively associated. Our results support the hypothesis that the number of contacts among crayfish at high density levels decreased when habitat complexity increased and food was unlimited. But, the importance habitat complexity and prey consumption depends on whether or not structure is available, not on the amount of structure. Once habitat structure is available for the predator, the amount of habitat complexity did not affect prey consumption in this study.

In conditions of high food levels and simple habitats, crayfish foraging time is reduced because of mutual interference. Moreover, aggression among animals is enhanced when food is found in a single patch (as in this study) than when food is distributed widely (Fraser et al. 1995). Different relationships may exist in environments where macrophytes provide habitat structure (Nystrom et al. 1996) and prey are evenly distributed.

By providing refuges, habitat structure may mediate the outcome of contests so that winners and losers in competition or predation can be anticipated (Hixon and Menge 1991; Caley and St. John 1996; Jones and Syms 1998). Increased crayfish density may lead to competitive interactions that reduce foraging time and ultimately prey consumption. Savino and Miller (1991) showed that highest feeding rates in the laboratory occurred when rocks were absent and when test tanks contained single crayfish.

When food was abundant, prey consumption per crayfish increased with increasing complexity at low and moderate crayfish densities. This finding suggests that an increase in habitat complexity producing an increase in food consumption will result in increased weight gains to individual cray-

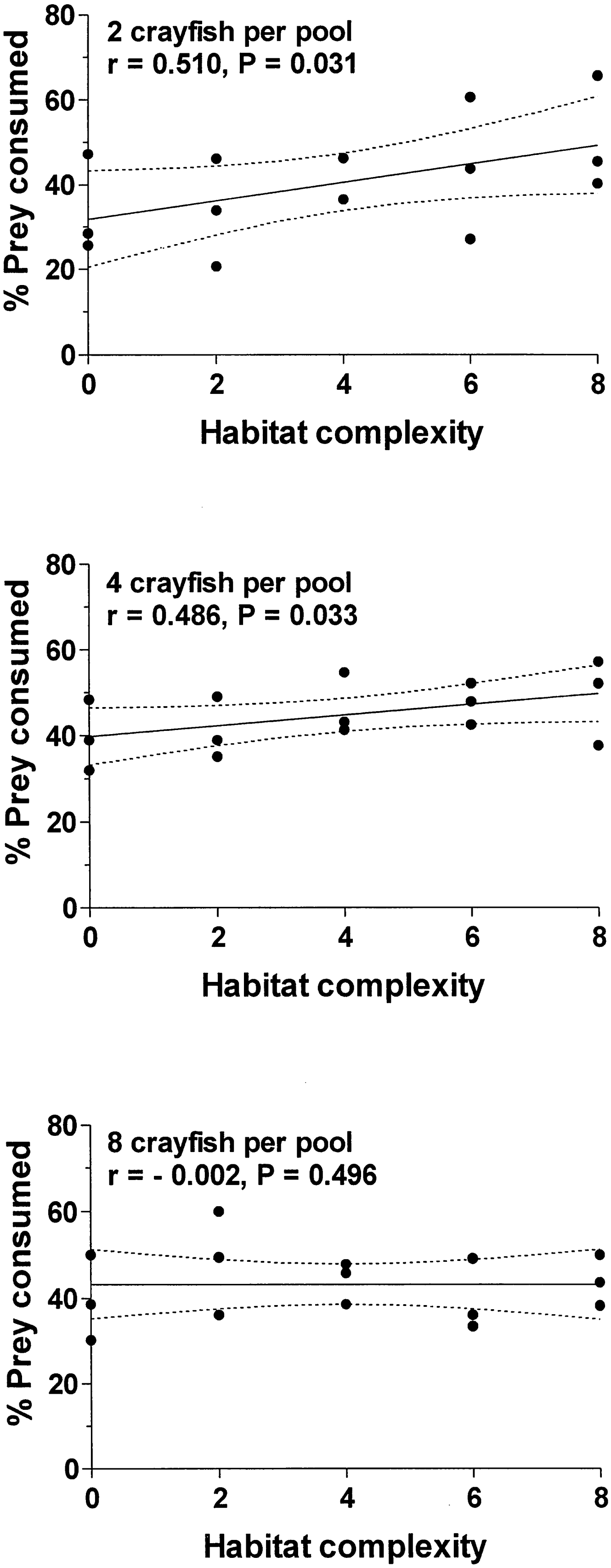

Fig. 2. Relationship between per cent of prey consumed per crayfish and habitat complexity for the three density treatments (2, 4, and 8 crayfish per pool) at high food levels. Linear *regression line* and 95% confidence interval are plotted for each case

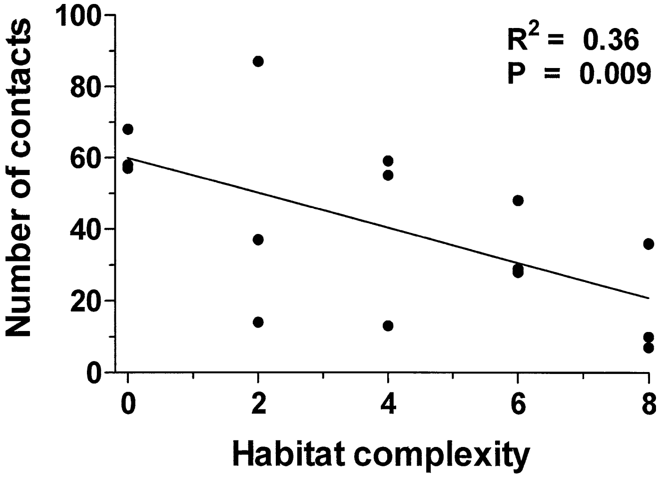

Fig. 3. Relationship between the number of contacts recorded between crayfish and habitat complexity when food was unlimited

fish. However, one might argue that crayfish in zero habitat complexity treatments could exhibit lower prey consumption because of the “stress” of open space regardless of the presence of others.

Interestingly, the number of contacts between and among crayfish declined with increasing habitat complexity (Fig. 3), yet there was no significant difference between per cent of prey consumed and habitat complexity for the highest crayfish density treatment in unlimited food conditions (Fig. 2, bottom panel). Other factors may account for these findings. First, observations of our videotapes revealed that one or two crayfish monopolised the prey. Second, although the inverted flower pots provided an increased number of hiding locations behind structures, crayfish were never completely hidden within an enclosure. Moreover, the inverted pots reduced the available surface area on the bottom of the pool. Third, the excretion of chemical compounds produced to inhibit food acquisition by subordinates may reduce consumption when food resources appear to be abundant (Brown et al. 1995). Clearly, additional experiments are needed to resolve these relationships.

Although it is feasible that high densities of predators may result in lower per capita consumption of prey because of mutual interference among predators, Hassell (1978) reported that parasitoid wasps and predatory mites react to aggregations of predators by dispersing. Thus, the dispersal period represents time away from foraging. Crayfish also disperse from high density to low density areas (Bovbjerg 1964). Crayfish, however, are highly aggressive and engage in agonistic contests in the laboratory and the field (Bovbjerg 1959; Guiasu and Dunham 1997). In our study, the greatest difference in the number of contacts among crayfish was between the simplest and most complex habitats; more interactions occurred in simpler habitats.

Our study focused on the behaviour of predators and a single predator species interaction with prey. Multiple predators, however, affect prey in a more complex manner (Sih et al. 1998; Swisher et al. 1998). For example, Miller et al. (1992) showed that in the presence of the slimy sculpin (*Cottus cognatus*), crayfish predation on trout eggs was reduced 50% and crayfish spent more time in refuges. Nevertheless, we showed that through the manipulation of habitat complexity and food levels both food consumption and aggression among crayfish are altered. Although there was a difference between simple and complex habitats, there were no differences in food consumption at increasing levels of habitat complexity. These findings suggest that a minimal amount of habitat complexity can reduce predator-predator interactions, ultimately resulting in increased prey consumption.

Acknowledgements We thank Jan J.H. Ciborowski, Donna J. Giberson, Ray G. Poulin and an anonymous reviewer for their comments on the manuscript. Michelle Dobrin kindly provided field assistance.

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