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An increase in habitat complexity reduces aggression and monopolization of food by zebra fish (*Danio rerio*)

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Abstract: We tested the predictions that an increase in the structural complexity of a habitat causes both a decrease in aggression and the monopolization of resources. Groups of three zebra fish (*Danio rerio*) were allowed to compete for food in a complex habitat with simulated vegetation and in a simple habitat with no vegetation. As predicted, both the levels of aggression by the dominant fish ($P = 0.050$) and the coefficient of variation of the amount of food eaten within a group ($P = 0.020$), a measure of food monopolization, were lower in the complex habitat than in the simple one. Fish that chased competitors more frequently ate more food in both habitats, but the relationship was stronger in the simple than in the complex habitat. Our results suggest that aggression is less useful as a mode of competition in habitats with greater structural complexity. Manipulating the structural complexity of the habitat may be a practical way of controlling the intensity of aggression and resource monopolization in groups of animals.

Résumé : Nous avons éprouvé les hypothèses selon lesquelles une augmentation de la complexité structurale d'un habitat peut entraîner à la fois une diminution de l'agressivité et une réduction de la monopolisation des ressources. Des groupes de trois poissons-zèbres (*Danio rerio*) ont été mis en présence de nourriture dans un habitat complexe avec de la végétation simulée, ou dans un habitat simple sans végétation. Tel que prévu, et l'agressivité des poissons dominants ($P = 0{,}050$) et le coefficient de variation de la nourriture mangée au sein d'un groupe ($P = 0{,}020$), une mesure de la monopolisation de la nourriture, étaient plus faibles dans le milieu complexe que dans le milieu simple. Les poissons qui poursuivaient les compétiteurs plus souvent ont mangé plus de nourriture dans les deux milieux, mais la relation était plus robuste dans l'habitat simple que dans l'habitat complexe. Nos résultats indiquent que l'agressivité est moins utile comme mode de compétition dans les habitats de structure plus complexe. La manipulation de la complexité structurale d'un habitat peut s'avérer une méthode pratique de contrôle de l'intensité de l'agressivité et de la monopolisation des ressources chez des groupes d'animaux.
[Traduit par la Rédaction]

Introduction

The ability of an animal to defend and monopolize resources is thought to be partly related to the structural complexity of its habitat. Increases in habitat complexity may increase the costs of defence by making it more difficult to detect and expel intruders from a territory (Schoener 1987; Eason and Stamps 1992). Intruders that are not immediately expelled consume food on the territory and reduce the growth rate of the territory owner (e.g., Stamps 1984; Stamps and Eason 1989). In addition, the longer an intruder remains on a territory, the more difficult it is to evict from the territory (Krebs 1982). Consequently, an increase in the structural complexity of a habitat is predicted to decrease territory size or the time allocated to patrolling and aggression (Schoener 1987).

Habitat complexity may also affect the monopolization of resources, the primary benefit of aggression. The foraging efficiency of fishes typically declines as the complexity of the

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habitat, usually submerged vegetation, increases (Savino and Stein 1982; Gotceitas and Colgan 1989). The rates of attack and capture decline (Diehl 1988), presumably because the visual barrier provided by the vegetation makes it difficult for the predators to fixate visually on prey (Savino and Stein 1982). Hence, dominant individuals may be less able to monopolize food in complex habitats, where foraging is a more difficult and time-consuming task.

Few studies have manipulated the structural complexity of a habitat while monitoring some aspect of resource defence. Juvenile lizards (*Anolis aeneus*) defended smaller territories in habitats with low rather than high visibility (Eason and Stamps 1992). Similarly, juvenile Atlantic salmon, *Salmo salar*, decreased the size of their territories when the addition of boulders increased the topographic complexity of the substrate (Kalleberg 1958). The purpose of our study was to test the predictions that both levels of aggression and monopolization of resources decrease in structurally complex habitats. We allowed groups of three zebra fish (*Danio rerio*) to compete for food in a structurally complex habitat, where we added simulated vegetation, and in a simple habitat with no vegetation.

Methods

Fifty juvenile zebra fish were purchased from a pet store and transferred to two 75-L tanks (60 cm long × 30 cm wide × 40 cm high) on a 12 h light : 12 h dark photoperiod. The fish were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care. Each tank contained a box filter, an undergravel filter, and aged tap water at 24°C. Fish were fed flake food and previously frozen brine shrimp. Experimental groups were formed by haphazardly selecting one large (0.907 ± 0.197 g ($\bar{x}$ ± SD)), one medium-sized (0.618 ± 0.220 g), and one small (0.358 ± 0.093 g) fish from the stock tanks. Size differences within the group were selected to facilitate the recognition of individuals.

Two 40-L experimental tanks (50 × 25 × 32 cm) were equipped with an aquarium heater, an undergravel filter, and gravel to a depth of 3 cm. The top of each tank was covered with black Plexiglas, whereas the back and ends were covered with white paper. Other conditions were as described for the stock tanks. The experimental tank was divided into two equal chambers by a piece of black Plexiglas. A 4 × 4 cm opening could be uncovered, allowing fish to pass between the two chambers. Three holes (0.5 cm in diameter) were drilled through the Plexiglas lid over each chamber. The holes were arranged 16 cm apart to form an equilateral triangle centred over the middle of each chamber. Small funnels were inserted into the six holes to facilitate the addition of food.

One of the chambers was randomly selected to receive the addition of simulated vegetation. Twelve strips (25 × 2 cm) of buoyant plastic garbage bag were embedded in the gravel in this "complex" habitat. The 12 strips were spaced 4 cm apart in a 3 × 4 arrangement, with their wide side perpendicular to the front of the tank. The vegetation made it more difficult for fish to swim in a straight line and to see prey and competitors.

A group of fish was added to the experimental tank and allowed to frequent both habitats. Fish were fed 36 previously frozen adult brine shrimp each day. Each shrimp was suspended in water in an eyedropper and dispensed into the tank through one of the funnels. On the first 2 days in the tank, the fish were fed in the simple habitat. On average, one prey was dropped into the tank every 15 s over a 9-min feeding period. The funnel receiving the food was randomly chosen. We also randomly varied the exact time of food arrival by 0, 1, 2, or 3 s before or after the 15-s mark during each minute to ensure that fish could not predict the exact time of feeding.

On day 3 we randomly selected one habitat for feeding. The fish were gently coaxed into the appropriate habitat using a dip net and the door between the two habitats was closed. The door was reopened after feeding and the fish were free to use both habitats. We alternated the habitat receiving food for the next 5 days; the total was 3 days in each habitat. The fish showed no obvious bias towards either habitat between feeding periods. During feeding trials, an observer sat quietly in front of the tank recording the number of prey eaten and the number of chases initiated by each fish. A chase was defined as a unidirectional burst of swimming directed towards a conspecific. In total, five groups of three fish each were used in the experiment.

We used paired *t* tests to compare the average data from the three feeding trials in the complex habitat with the average data from the three feeding trials in the simple habitat. We used one-tailed tests of the a priori prediction that aggression levels and monopolization rates would be lower in the complex than in the simple habitat. All other tests were two-tailed.

Results

During feeding periods the dominant fish typically circled under the feeding area, chasing competitors away. On average, the dominant fish accounted for 82% of chases during feeding trials. Interestingly, the chase rate within a group was not significantly correlated with body mass (Spearman's $r_s = 0.400$, $n = 15$, $P = 0.140$; both ranked within groups).

As predicted, the rate of aggression by dominant fish (chases/min) was higher in the simple (7.28 ± 1.71 ($\bar{x}$ ± SE)) than in the complex (3.70 ± 0.95) habitat (paired $t = 2.12$, $n = 5$, $P = 0.050$, one-tailed test). A similar but weaker trend (paired $t = 1.96$, $n = 5$, $P = 0.061$) was observed in the total rate of aggression by all three fish (complex habitat, 7.81 ± 1.52; simple habitat, 4.43 ± 0.76).

Because the total number of prey eaten during feeding trials did not differ significantly between the simple ($\bar{x}$ = 77%) and the complex ($\bar{x}$ = 72%) habitats (paired $t = 1.35$, $n = 5$, $P = 0.25$), the coefficient of variation (CV = (SD/mean) × 100) was a suitable measure of the monopolization of food in our study (see Ruzzante et al. 1996). As predicted, the monopolization of food was higher in the simple (CV= 94.7 ± 8.4 ($\bar{x}$ ± SE)) than in the complex (79.3 ± 5.4) habitat (paired $t = 3.00$, $n = 5$, $P = 0.020$, one-tailed test), primarily because dominant fish ate 60.7% of the food in the simple habitat compared with 51.9% in the complex habitat (paired $t = 2.13$, $n = 5$, $P = 0.050$, one-tailed test).

The best predictor of feeding success in the simple habitat was rank (i.e., chase rate). Fish that chased at a higher rate ate more food ($r_s = 0.94$, $n = 15$, $P < 0.0001$; both ranked within groups). This positive relationship between chase rate and feeding success was weaker, but still positive, in the complex habitat ($r_s = 0.60$, $n = 15$, $P = 0.018$). Body mass was not significantly correlated with feeding success in either the simple ($r_s = 0.10$, $n = 15$, $P = 0.72$) or the complex ($r_s = –0.20$, $n = 15$, $P = 0.47$) habitat.

Discussion

Our study contributes to the small but growing literature suggesting that an increase in the structural complexity of a habitat reduces the usefulness of aggression as a means of competition. The clearest effect of an increase in habitat complexity is a reduction in territory size (Kalleberg 1958; Eason and Stamps 1992). The results of our study suggest that an increase

in habitat complexity also reduces aggression and the ability of dominant individuals to monopolize resources, even in species like the zebra fish that does not defend classical territories.

A decrease in visibility is thought to be the proximate factor causing aggression and (or) territory size to decrease in complex habitats (Eason and Stamps 1992). Perhaps the clearest illustration of the effect of visibility on rates of aggression is in the mudskipper, *Boleophthalmus boddarti*, a gobiid fish. Mudskippers defend feeding territories on mud flats, two-dimensional habitats with little structural complexity (Clayton 1987). At high densities, mudskippers surround their territories with mud walls 30–40 mm in height, apparently as a visual barrier between territorial neighbours. Removal of the walls causes an increase in aggression between neighbours (Clayton 1987).

The effect of habitat complexity on aggression may be useful to applied ecologists. An increase in the structural complexity of habitats should allow them to support higher densities of territorial animals (Kalleberg 1958) and help reduce the aggression that is often observed in aquaculture facilities, zoos, and groups of domestic animals (e.g., Ruzzante 1994; Fraser et al. 1995).

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