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, 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

Received June 25, 1997. Accepted October 21, 1997.

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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 hap- and aged tap water at 24°C. Fish were fed flake food and previously frozen brine shrimp. Experimental groups were formed by hap-

**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 ($7.28 \pm 1.71$ (SE)) than in the complex ($3.70 \pm 0.95$) habitat (paired $t = 2.12$, $P = 0.050$, 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, $7.81 \pm 1.52$; simple habitat, $4.43 \pm 0.76$).

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 (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简单 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).

**Acknowledgements**

This study was financially supported by the Department of Biology at Acadia University and a Research Grant from the Natural Sciences and Engineering Research Council of Canada to J.W.A.G. For advice with experimental design, S.P.B. thanks Søren Bondrup-Nielsen, Tom Herman, and the graduate students in the Acadia Tutorial in Behavioural Ecology. We thank two anonymous reviewers for helpful comments on the manuscript.

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