

NOTE

Manipulating territory size via vegetation structure: optimal size of area guarded by the convict cichlid (*Pisces, Cichlidae*)

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Abstract: To test the predictions of optimal territory size models, we attempted to manipulate the size of area that a dominant convict cichlid fish (*Archocentrus nigrofasciatus*) would defend around a food patch by placing simulated vegetation at three different distances from the edge of the patch (0, 11, and 22 cm). As expected, the size of area defended against four smaller intruders increased as the vegetation was moved farther from the patch. Consistent with optimal territory size models, both the costs of defence, measured as chase radius and chase rate, and the benefits of defence, measured as the amount of food eaten by the defender, increased with the distance of the vegetation from the patch. Growth rates of the defenders, however, did not differ among the treatments, perhaps because the benefits of monopolizing food were balanced by the costs of defending a larger area. Our data support the hypothesis that the size of a guarded area around an ephemeral resource patch affects both the costs and benefits of defence.

Résumé : Pour éprouver les prédictions des modèles de taille optimale du territoire, nous avons tenté de manipuler l'aire que défendrait un cichlide à bande noire (*Archocentrus nigrofasciatus*) dominant autour d'une source de nourriture, en plaçant de la végétation simulée à trois distances de la bordure de la source de nourriture (0, 11 ou 22 cm). Comme on pouvait s'y attendre, l'aire défendue contre quatre intrus de plus petite taille augmente à mesure que la végétation est éloignée de la source de nourriture. En accord avec les modèles de taille optimale du territoire, les coûts associés à la défense du territoire, soit le rayon de chasse et la vitesse de chasse, de même que les bénéfices, évalués d'après la quantité de nourriture ingérée par le défenseur, augmentent en fonction directe de la distance de la végétation à la source de nourriture. Le taux de croissance du défenseur s'est cependant avéré le même dans tous les traitements, peut-être parce que les bénéfices reliés au monopole d'une source de nourriture additionnelle sont équivalents aux coûts associés à la défense d'un territoire plus grand. Nos données appuient l'hypothèse selon laquelle la taille d'une aire surveillée autour d'une ressource éphémère affecte à la fois les coûts et les bénéfices de la défense de cette aire.

[Traduit par la Rédaction]

Introduction

Optimal territory size models (e.g., Hixon 1980, 1987; Schoener 1983, 1987) predict that a defender's fitness will be a function of its territory size. Because larger territories contain more resources but are also costlier to defend, the optimal territory is predicted to be of intermediate size (Davies 1978; Wittenberger 1981). Optimal territory size models are typically tested by showing that animals adjust the size of their territories in an inverse relationship to changes in food density or intruder pressure (reviewed in Praw and Grant 1999). Few studies, however, have tested the more fundamental prediction that the fitness of the defender will be a

function of territory size or that the optimal territory will be of intermediate size (but see Carpenter et al. 1983; Praw and Grant 1999), perhaps because of the difficulty of manipulating the size of a guarded area.

While relatively permanent territories may be the best known form of resource defence, animals often guard (sensu Chapman and Kramer 1996) ephemeral concentrations of resources. Examples of such guarded patches, some of which may be mobile, include mates, carcasses, and broods. A guarded patch is fundamentally different from a traditional territory because a larger guarded area does not contain more resources than a smaller guarded area, whereas a larger territory usually contains more resources than a smaller territory. However, guarding a larger exclusion zone around a fixed patch may increase the defender's monopolization of the resource in the patch by keeping potential competitors farther away. Hence, optimal territory size models may also apply to guarded areas around resource concentrations. Perhaps the best evidence supporting the concept of an optimal size of guarded area is the behaviour of pairs of *Cichlasoma maculicauda* parents; they varied the size of the guarded area around their offspring according to the susceptibility of

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those offspring to different species of predators (Perrone 1978). The increased benefits of keeping dangerous predators farther away apparently more than compensated for the increased costs of defending a large exclusion zone around the brood.

In a previous study, Praw and Grant (1999) provided evidence of an optimal territory size for convict cichlids (*Archocentrus nigrofasciatus*). They manipulated territory size by allowing dominant convict cichlids to defend food patches that varied 121-fold in size. Larger territories contained more food but were more costly to defend, so the fish defending intermediate-sized territories grew the fastest. The objective of this parallel study was to determine the consequences to the defender of differences in the size of a guarded area around a food patch containing a constant amount of food. We began by attempting to manipulate the size of the guarded area around the food patch by placing simulated vegetation at different distances from the patch. The vegetation was intended to provide hiding places for intruders and obstruct the defender's view of approaching intruders. Hence, we expected the size of the guarded area to increase with the distance of the vegetation from the patch, as predicted by Eason and Stamps (1992). If our manipulation of the size of the guarded area was successful, we expected the gross benefits of defence, measured as the amount of food eaten by the defender, and the costs of defence, measured as chase radius and chase rate, to increase with initial increases in the size of the guarded area. We also expected the net benefits of defence, measured as the growth rate of the defender, to increase with initial increases in the size of the guarded area.

We used the convict cichlid as our test species. In the wild, convict cichlids defend nesting sites and offspring (Wisenden 1994, 1995), but defence of feeding territories has not been reported. However, dominant fish readily defend food patches in the laboratory, presumably because the food is economically defensible (e.g., Grant and Guha 1993; Grand and Grant 1994; Praw and Grant 1999), as are offspring in the wild. Growth rate should be an important component of fitness for convict cichlids because larger males monopolize breeding sites (Wisenden 1995) and mate with larger females (Keenleyside 1985), whereas larger females are more fecund (Nuttall and Keenleyside 1993) and out-compete smaller females for access to males with breeding sites (Wisenden 1995).

Methods

Experimental subjects

Approximately 200 juvenile convict cichlids were held in 10 stock tanks. These fish were the descendants of crosses made approximately three generations previously between laboratory fish and wild fish from Costa Rica. Groups of five fish were haphazardly selected from the stock tanks so that the body mass of the largest fish was at least 25% larger than that of any of the other four fish. On average, the mass of the smallest fish was 57.6% of that of the largest fish in the group. We expected the large fish to defend the food patch (see below) and the four smaller fish to act as intruders. These groups were assigned at random to one of three treatments (see below). In total, 105 fish (i.e., 21 groups of

5 fish) were used in the experiment (body mass = 2.40 ± 0.55 g (mean \pm SD); range = 1.52–3.76 g).

Experimental procedures

Two $90 \times 45 \times 41.5$ cm ($l \times w \times h$) fish tanks were used for the experiment. Each tank contained an under-gravel filter, a heater, two airstones, and gravel to a depth of 3 cm, and were filled to 2 cm from the top edge with aged tap water. The glass on the back and sides of the tanks was covered with white paper to minimize disturbance of the fish and facilitate videotaping. The water temperature was kept constant at 28–29°C.

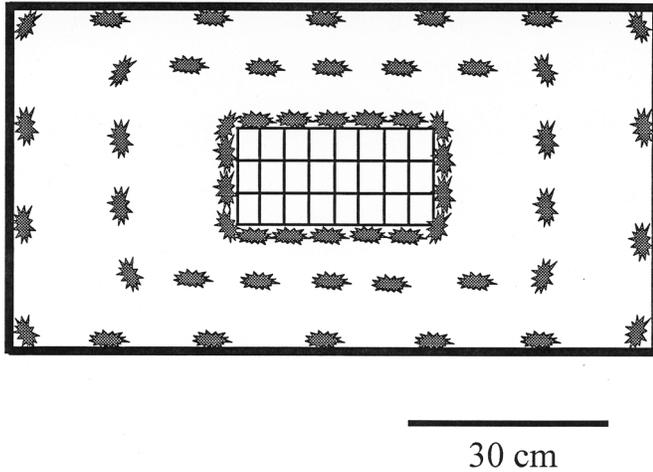
Food patches (16×31 cm) were made from plastic ice-cube trays containing 24 “cells.” A base for each patch, which was identical in size to the food patch, was attached to the under-gravel filter. This base was centred in the aquarium and stayed permanently in the tank. The food patch was attached to the base only during feeding periods.

We attempted to manipulate the size of the guarded area around the patch by placing simulated plants at three distances from the edge of the patch: 0, 11, and 22 cm (Fig. 1). The simulated vegetation consisted of 18 plants, each with 14 “leaves” (each leaf was 15 cm in length and 1 cm in width) made from plastic garbage bags. Each plant was tied to a glass marble and then “planted” in the gravel.

We completed 7 replicates of each treatment for a total of 21 groups between 20 November 1999 and 28 February 2000. Each group was subjected to one of the three treatments for a 7-day trial. At 07:30 on day 1 we weighed the fish and placed one group of five fish in each experimental tank. Fish were fed twice a day (at 10:00 and 15:00) from days 1 to 6 by placing the food patch in the tank for 30 min. On days 1–3 and the morning of day 4, the fish were trained to feed from the patch. Forty “Fry Feed Kyowa” pellets (1000 μ m in diameter; proximate composition: crude protein not less than 55%, crude fat not less than 10%, crude fibre not less than 4%, and crude ash not more than 17%) were placed in each patch (2 pellets per cell); 4 cells out of 24 were filled with gravel to stabilize the patch. During training, half the maximum ration was given, to minimize growth; we doubled the ration to 80 pellets for the second feeding on day 4 and for days 5 and 6. We set the ration at 80 pellets to be able to detect growth (Praw and Grant 1999), promote competition, and yet not satiate the fish (see Grant et al. 2002). On days 5 and 6, the morning feeding trial was videotaped from directly above the aquarium. On the morning of day 7, the fish were weighed (± 1 mg, using a Mettler PM460 balance) for the second time and then placed in an aquarium for used fish.

During videotaping of a trial, an observer (C.B.) sitting 2 m in front of the aquarium called out the occurrence of each chase to facilitate data collection. At the same time, the locations of the chases were recorded on a top-view drawing of the tank. A chase was defined as accelerated swimming by the defender towards an intruder, which immediately fled. The location of the chase was the position of the intruder when the defender initiated the chase; the chase radius was calculated as the distance (cm) from the middle of the patch to the location of the chase. Behavioural data retrieved from the videotapes included the number of pellets eaten by the defender and the intruders. C.B. also noted the time when all

Fig. 1. Top view of the experimental tank, showing the three treatments; 18 simulated plants were placed 0, 11, or 22 cm from the edge of the feeding patch.



the food had been eaten, usually within 10 min (4.98 ± 3.3 min (mean \pm SD)), to test whether the defender's behaviour changed after the food was eaten. From the chase-radius data we calculated convex polygons that included 95% of all chases. We calculated the size of the area guarded by the defender by means of a computer digitizing system.

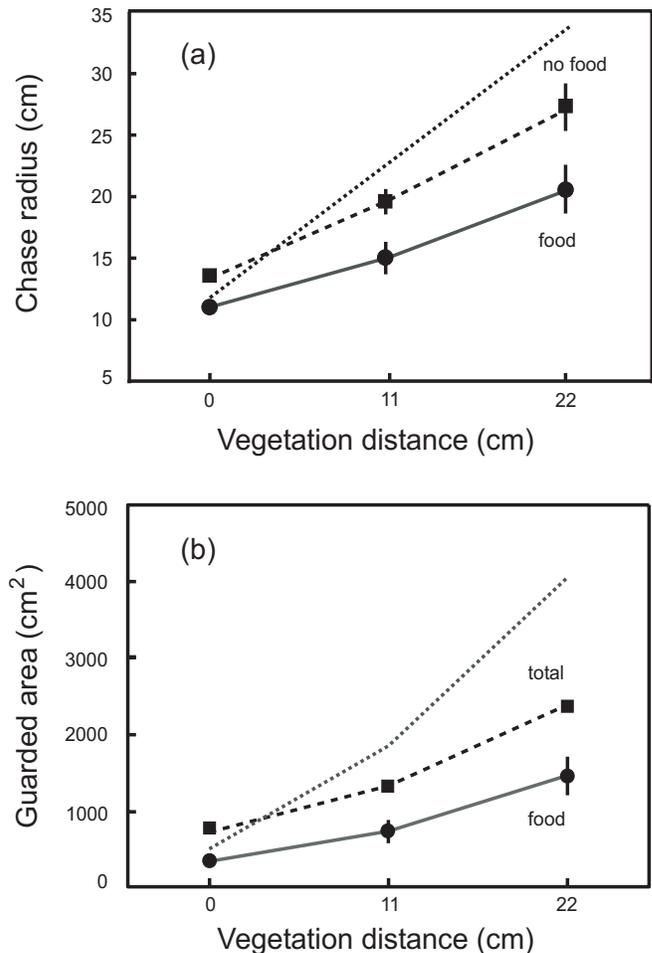
The data did not require transformation to meet the assumptions of parametric tests.

Results

The defender usually hovered over the centre of the patch and vigorously chased the intruders away. The simulated vegetation provided hiding places for the intruders to escape the defender and refuges from which to sneak into the patch.

As expected, the guarded area increased in size as the simulated vegetation was moved farther from the patch (Fig. 2). The defender's average chase radius increased significantly with the distance of the vegetation from the patch (two-way repeated-measures ANOVA, $F_{[2,18]} = 11.15$, $P < 0.001$; Fig. 2a). Chase radius also increased after all the food was eaten (two-way repeated-measures ANOVA, $F_{[1,18]} = 40.26$, $P < 0.001$; Fig. 2a), but there was no interaction between vegetation distance and the presence or absence of food ($F_{[2,18]} = 2.98$, $P = 0.076$). The guarded area also increased with vegetation distance (two-way repeated-measures ANOVA, $F_{[2,18]} = 34.62$, $P < 0.001$; Fig. 2b). The guarded area was also larger when measured for the complete trial than just when food was present ($F_{[1,18]} = 48.23$, $P < 0.001$; Fig. 2b), because the chase radius increased after the food was eaten and because the size of a minimum convex polygon increases with sample size (Schoener 1981). Again there was no significant interaction between the two main effects ($F_{[2,18]} = 2.97$, $P = 0.077$). In summary, the key assumption of our study was met: we were able to manipulate the area guarded by the defender by varying the distance of the vegetation from the patch. In the 0-cm treatment, in particular, the area guarded by the defender appeared to be severely constrained by the vegetation; the defender occasionally chased intruders into the vegetation.

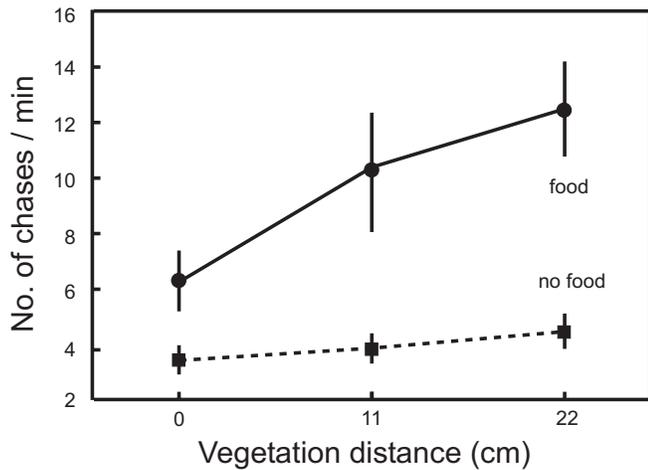
Fig. 2. (a) Chase radius (mean \pm 1 SE, $n = 7$) of the defender in relation to vegetation distance during feeding trials when food was present ("food") and after all the food was eaten ("no food"). The dotted line represents the average distance of the vegetation from the centre of the patch. (b) Area (mean \pm 1 SE, $n = 7$) guarded by the defender (minimum convex polygon containing 95% of all chases) when food was present ("food") and during the complete 30-min feeding trial ("total") in relation to vegetation distance. The dotted line represents the area within the rectangle of simulated plants.



Chase rate, the second component of the costs of defence, also increased with vegetation distance (two-way repeated-measures ANOVA, $F_{[2,18]} = 3.70$, $P = 0.045$; Fig. 3). While vegetation distance appeared to have a greater effect when food was present, there was no significant interaction between vegetation distance and the presence or absence of food ($F_{[2,18]} = 2.46$, $P = 0.11$). In contrast to the chase radius, the chase rate decreased after all the food was eaten ($F_{[1,18]} = 34.31$, $P < 0.001$).

The number of pellets eaten by the defender, a measure of the gross benefits of defence, increased with vegetation distance (one-way ANOVA, $F_{[2,18]} = 3.89$, $P = 0.040$; Fig. 4a). Defenders ate about 40% of the food when the vegetation abutted the food patch compared with about 56% when the vegetation was moved 22 cm away. This significant trend, however, did not translate through to the net benefits of defence, since the mass gain of the defender did not differ

Fig. 3. Chase rate (mean \pm 1 SE, $n = 7$) of the defender in relation to vegetation distance during feeding trials when food was present (“food”) and after all the food was eaten (“no food”).



significantly among treatments (one-way ANOVA, $F_{[2,18]} = 1.49$, $P = 0.25$; Fig. 4b). The mass gain of intruders also did not differ significantly among vegetation distances (one-way ANOVA, $F_{[2,18]} = 0.15$, $P = 0.862$; Fig. 4b).

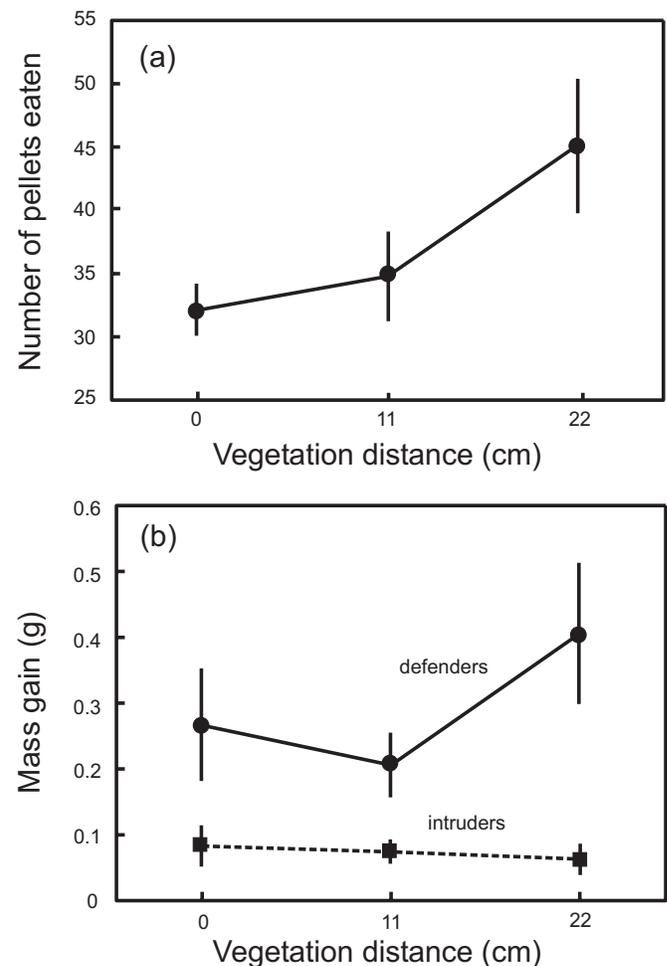
Not surprisingly, the combined mass gain of the defender and the four intruders increased with the number of pellets eaten (analysis of covariance, $t = 3.83$, $n = 42$, $P < 0.001$). Moreover, there was no significant difference between defenders and intruders in either the slope ($t = 0.04$, $n = 42$, $P = 0.97$) or the elevation ($t = 0.40$, $n = 42$, $P = 0.69$) of the relationship between mass gain and number of pellets eaten. Hence, the best predictor of mass gain was the number of pellets eaten (mass gain (g) = $0.00947 \times$ number of pellets eaten $- 0.0872$; $r^2 = 0.269$, $P < 0.001$). To determine whether the defender's behaviour influenced the mass gain of either the defender or the intruders, we included the chase radius and chase rate of the defender (both with and without food) in a multiple regression after the effect of the number of pellets eaten was first entered in the model. Only the chase rate when food was present had any effect: it was negatively, but not significantly, related to the defender's growth rate (multiple regression, $t = 1.75$, $n = 21$, $P = 0.097$). In addition, the defender's behaviour had no significant effect on the growth rate of the intruders (multiple regression, all $P > 0.10$) after the effect of the number of pellets eaten was considered.

Discussion

Our ability to manipulate the size of the area guarded by convict cichlids contributes to the small amount of literature on the effects of habitat visibility on territory size (see Eason and Stamps 1992). In previous studies, juvenile Atlantic salmon (*Salmo salar*; Kalleberg 1958), lizards (*Anolis aeneus*; Eason and Stamps 1992), and rainbow trout (*Oncorhynchus mykiss*; Imre et al. 2002) decreased the size of their territories in low-visibility environments.

We think our manipulation was successful for three reasons. First, the simulated vegetation provided hiding places, allowing intruders to avoid eliciting aggression from the defender. When the vegetation was close to the patch, the in-

Fig. 4. Effect of vegetation distance on the number of pellets eaten by the defender (a) and mass gain of the defender and the average mass gain of the four intruders in each tank (b) (mean \pm 1 SE, $n = 7$).



truders could safely hide within a few body lengths of the food patch. Second, even when the intruders were seen by the defender, the vegetation allowed them to escape the defender's aggression without having to move far from the patch. Third, an overzealous defender that chased intruders beyond the row of vegetation would quickly lose food to other intruders who would quickly dart in from behind other plants. After all the food was eaten, the defenders increased the size of their guarded area, perhaps because they no longer had to worry about the cost of stolen food (also see Praw and Grant 1999). House mice, *Mus domesticus*, were also less effective at defending territories in a structurally complex environment than in an open environment (Gray et al. 2000).

As assumed by optimal territory size models (e.g., Hixon 1980, 1987; Schoener 1983, 1987), the chase rate increased with the size of the guarded area. As the vegetation was moved farther from the patch, the defenders had a clearer view of approaching intruders, and hence increased their chase rate. After all the food was eaten, intruders approached the food patch less frequently, causing the chase rate to decline.

The defender increased its share of the food as vegetation distance increased, supporting the prediction that the gross

benefits of defence are a function of the size of the guarded area. Dominant zebrafish, *Danio rerio*, were also able to increase their share of food in environments with less structural complexity, presumably because aggressive behaviour was more effective in these high-visibility environments (Basquill and Grant 1998; also see Gray et al. 2000). Despite the trends in monopolization of food, vegetation distance did not affect the growth rate of the defenders, perhaps because the gross benefits of guarding a larger area were balanced by the increased costs of chasing more often and farther when vegetation distance was greater. Alternatively, our 2.5-day trials on full rations may have been too short to detect growth differences among the treatments. In contrast, Prawn and Grant (1999) were able to detect significant differences in the growth rate of convict cichlids defending patches of different sizes, but their trials were twice as long as those in our study.

For a given number of pellets eaten, the intruders grew at the same rate as the defender. In contrast, a previous study in a high-visibility environment showed that subordinates grew less efficiently than dominant convict cichlids, presumably because of social stress (Prawn and Grant 1999; see also Abbott and Dill 1989). Our intruders may have had relatively low levels of stress because they were able to hide easily from the defender. Manipulating the structural complexity of a habitat may be an effective way of controlling the amount of aggression in groups of animals. An increase in habitat structural complexity may reduce the rate of aggression (e.g., Sundbaum and Näslund 1998), the effectiveness of aggression (Basquill and Grant 1998), and, hence, the stress levels of subordinate animals in a group.

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