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Optimal territory size in the convict cichlid (Cichlasoma nigrofasciatum)

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A Thesis

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Abstract

Optimal territory size in the convict cichlid (Cichlasoma nigrofasciatum)

Simple models of optimal territory size have most commonly been tested qualitatively by demonstrating that an increase in food abundance or intruder pressure causes a decrease in territory size. However, the most fundamental predictions of the theory have rarely been tested: i.e. the fitness of the defender changes with territory size and the optimum occurs at a territory of intermediate size. I tested these predictions by measuring the growth rate of convict cichlids (Cichlasoma nigrofasciatum) defending food patches that differed in area by more than an order of magnitude. Groups of five fish competed for a food patch of a given size over a 10-day period. I assumed one large fish would defend the food patch and that the four smaller fish would act as intruders. As predicted, the growth rate of the defender first increased and then decreased with increasing patch size and was highest on an intermediate patch size. Costs of defence (chase rate, intruder pressure) increased linearly with patch size, whereas the benefits of defence (number of pellets eaten by the defender) increased in a decelerating way with increasing patch size. The best predictors of the defender's foraging success were patch size, chase radius, and chase rate; the most successful foragers fed on large patches, defended large territories, and chased few intruders. The growth rate of defenders increased with the number of pellets eaten and decreased as the number of intruders on their patch increased. Taken together, these results provide strong support for the assumptions and predictions of the optimal territory size model.

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Introduction

When competing for resources, animals often establish a territory, a more or less exclusive area defended by an individual or a group (Davies & Houston 1984). Brown (1964) revolutionized the study of this phenomenon when he suggested that territories will only occur when the benefits of defence exceed the costs, or when the net benefits of defence exceed the net benefits of an alternative strategy, such as scrambling for the resource. Brown's concept of economic defendability stimulated biologists to consider the environmental circumstances in which territoriality will occur.

This optimality approach suggests that territory size will also be determined by the costs and benefits of defence. Benefits are considered to be resources available from the territory such as food, potential mates, nest sites, and shelter, whereas costs include the energetic costs of defending the territory and the increased risk of injury and predation when engaged in defence (Brown 1964; Brown & Orians 1970; Stamps 1994). Both benefits and costs are assumed to increase with increasing territory size and may intersect at two different sizes (Fig. 1a). The intersections create upper and lower thresholds of territory size, between which the benefits of defence exceed the costs. Hence, this economic approach predicts that (i) only a range of territories will be economically defendable, and (ii) an optimal territory size, the territory size where the positive difference between the benefit and cost of defence is maximized, exists. Optimal territory size is also predicted to decrease when benefits (Fig. 1b) or costs (Fig. 1c) increase.

The simple optimal territory size model has been tested most commonly by determining the effect of manipulating food or intruder density on territory size. As predicted, most studies have shown that territory size decreases as food density increases (e.g. in rainbow trout *Oncorhynchus mykiss*, Slaney & Northcote 1974; iguanid lizards *Sceloporus jarrovi*, Simon 1975; rufous hummingbirds *Selasphorus rufus*, Gass et al. 1976, Kodric-Brown & Brown 1978; nuthatches *Sitta europaea*, Enoksson & Nilsson 1983; caddisflies *Leucothrichia pictipes*, Hart 1985; and grey plover *Pluvialis squatarola*, Turpie 1995) or as competitor density increases (e.g. in sanderlings *Calidris alba*, Myers et al. 1979; coho salmon *Oncorhynchus kisutch*, Dill et al. 1981; butterflyfish *Chaetodon multicinctus*, Tricas 1989; black-shouldered kite *Elanus caeruleus*, Dunk & Cooper 1994; and Anna's hummingbirds *Calypte anna*, Eberhard & Ewald 1994).

The most fundamental prediction of the simple optimal territory size model, that fitness of the territory holder changes with territory size, has rarely been tested. Ideally, one would want to measure the fitness (e.g. growth rate) of animals defending territories of different sizes under the same environmental conditions. The simple model predicts that animals defending a territory of intermediate size will have the highest fitness (Fig. 1). These predictions have rarely been tested because it is difficult to "force" an animal to defend a territory of a given size. Perhaps the best demonstration of a correlation between territory size and fitness was provided by Carpenter et al. (1983). They followed rufous hummingbirds defending territories over several days in a new environment. One bird adjusted its territory size to increase its daily growth rate over a five day period (Fig. 2).

However, the behaviour of the other four birds in the study, not shown in Fig. 2, was highly variable.

A major shortcoming of studies of optimal territory size is that the shapes of the cost and benefit curves are usually not known. The predicted change in optimal territory size with changing environmental conditions depends crucially on the shapes of these curves (Schoener 1983). For example, if the benefits increase at a monotonically decreasing rate, while the costs are steeply accelerated, a decrease in food density predicts an increase in optimal territory size (Fig. 1b). However, if the benefit curve is changed to increase linearly until a finite maximum, while keeping the same cost curve, a decrease in food density now predicts a decrease in optimal territory size (Schoener 1983).

In this thesis, I demonstrate that individual convict cichlids (Cichlasoma nigrofasciatum) defending territories of different sizes differ in growth rate (fitness) (Ware 1982; Bryant & Grant 1995). I assumed that the dominant fish in a tank would defend a territory similar in size to the food patch I provided. Territory size was manipulated by using food patches of different size. I attempted to control the shape of the benefit curve so that the amount of food increased with increasing patch size in a decelerating manner. I assumed that the costs of defence would increase with territory size, so that the optimal territory size would be of intermediate size (cf. Fig. 1a).

The specific objectives of my thesis were to test the assumptions that (1) territory size is similar to food patch size, (2) the costs of defence increase with patch size, (3) the benefits of defence increase in a decelerating way with patch size, and the predictions that

(4) growth rate varies as a function of patch size and (5) growth rate is highest for fish defending patches of intermediate size.

Methods

Experimental Subjects

Convict cichlids are ideal subjects for my study because they actively defend concentrations of food in the laboratory and grow quickly. In the wild, convict cichlids defend nesting sites and their young, but do not defend feeding territories (Wisenden 1994 & 1995). The fish used in this study were the descendants of crosses between laboratory stock and wild fish from Costa Rica. Only sexually immature fish were used to minimize any reproductive behaviour. All fish were kept in stock aquaria (60 x 30 x 35 cm) maintained at 30°C on a 11:13 light:dark photoperiod. Each aquarium had an undergravel filter, a fully submerged 100 W heater, light-coloured gravel to 3 cm in depth, and aged Montréal tap water. Fish in stock aquaria were fed "Fry Feed Kyowa" pellets *ad libitum* once or twice daily.

Thirty-two groups of five fish were formed, composed of one large individual, ranging in mass (nearest 1.0 mg) from 1600 to 2000 mg ($\bar{X}\pm SD=1778\pm93.74$, $N=32$), and four small fish, ranging in mass from 40 to 60% of the weight of the large fish ($\bar{X}\pm SD=852\pm105.15$, range=661 to 1128 mg, $N=124$). I was unable to measure the initial size of four intruders (see below). I expected the large fish to be the defender of the food patch (see below) and the four small fish to act as intruders (Grant & Guha 1993). The mean total length of the defenders and intruders was 47.3 and 37.7 mm, respectively.

Apparatus

The experiment was conducted in three aquaria (90 x 46 x 38 cm). Three sides of each aquarium were covered with white paper to minimize disturbance of the fish and to provide a suitable background for video recording. The top of each aquarium was covered with a black opaque Plexiglas lid. Other conditions were the same as in the stock aquaria.

I manipulated the size of the territory defended by the large fish by using food patches of different size. Patches were made from plastic ice-cube trays; each "cell" measured (5.3 x 3.8 x 3.5 cm). Each group was exposed to one of six patch sizes: 1, 9 (3x3), 25 (5x5), 49 (7x7), 81 (9x9), or 121 (11x11) cells measuring 3.8 x 5.3, 11.8 x 16.0, 19.9 x 27.0, 27.3 x 38.0, 35.5 x 49.0, and 43.5 x 60.0 cm, respectively (Fig. 3). Hereafter, I will refer to each patch size by their patch radius in terms of cells (i.e. 1, 3, 5, 7, 9, and 11). Food patches were centred on the bottom of the aquaria, attached directly to the undergravel filter, and then surrounded with the gravel. Each food patch was covered by a clear Plexiglas sheet into which small holes were drilled to allow food to be injected into each cell with 5 cc syringes. These Plexiglas sheets prevented fish from feeding while the patches were being stocked.

Experimental Procedure

I planned six replicates for each of six patch sizes (*N*=36). Due to a shortage of fish, I completed five replicates of patch size 1, 3, 5, and 9 and six replicates of patch sizes 7 and 11.

The amount of food in each patch was scaled to the maximum ration that a large fish could eat in one meal, approximately 34 mg. My goal was to feed the fish enough food for detectable growth without satiating the defender. I varied the amount of food ("Fry Feed Kyowa" pellets) so that it increased in a decelerating way with increasing patch size. The amount of food placed in each patch, twice a day, was 25, 50, 75, 95, 100, and 105% of the maximum ration for patch sizes 1, 3, 5, 7, 9, and 11, respectively (Fig. 4). With this shape of benefit curve, I expected the growth rate of the defenders to be highest at a patch size of 7. The food pellets (2.0 mm in diameter) were too big for the fish to eat, so they were ground into smaller pellets that varied in size from 0.5 to 1.5 mm in diameter. This allowed me to vary both the weight of food and the number of pellets in each treatment. Because growth rate in the first two replicates was low, I increased the maximum ration to 51 mg for the remaining replicates. The distribution of food pellets in the patch is shown in Table 1.

Each trial lasted 10 days. On Day 1, fish were food-deprived, weighed (see above), and placed into one of the three experimental aquaria. Fish were fed on Days 2 to 9. Air pumps were turned off and the black opaque Plexiglas lid was removed 15 min prior to feeding. A trial started when the Plexiglas sheet covering a food patch was slowly removed so as not to disturb the food pellets. Fish were then allowed to feed for 15 min. At the end of the trial, the clear Plexiglas sheet was replaced over the patch, the black opaque lid was then replaced, and the air pump turned back on.

On Days 2, 3, and 4 fish were given experience feeding in the patch. To ensure that little growth occurred during this acclimation phase, less than full rations of food were used. On Day 2, fish were fed 50% of their Day-5 ration at 1330 hrs. On Day 3 and 4, fish were fed 25% of their Day-5 ration, twice a day (1000 and 1700 hrs). The acclimation rations were not increased when the maximum ration was increased for the last four replicates. Feeding with the full rations, twice a day, began on Day 5 and continued until Day 9. On Day 10, I weighed the fish at 1330 hrs.

Behaviour was videotaped during the 15-min feeding period on the mornings of Days 7, 8, and 9. Fish were videotaped simultaneously from directly above the aquarium and from the front of the aquarium.

Mortality

Eight of 160 fish died during the trials; seven were intruders. The defender, which died before the first feeding, was immediately replaced. Of the seven intruders, five died on Day 2, were identified by weight, and then replaced by similar-sized intruders. The other two intruders died on Day 4 and 8 of the same trial. Both were replaced, but because of growth, I could not be sure of the initial weight of these intruders. Hence, I have initial weights for only 124 of 128 intruders (see above); i.e. 31 instead of 32 data points for all statistical tests including intruder growth rate.

Data Analyses

To test the assumption that costs of defence increase with patch size, I recorded, from the videotapes, the territory size of the defender, chase rate of the defender (chases/min), and intruder pressure (average number of intruders in the patch). Territory size was estimated in two ways. First, the actual area defended was estimated by calculating the average chase radius. A chase was defined as an accelerated movement by the defender towards an intruder. The radius of an individual chase was the distance (cm) between the centre of the patch and the intruder when the defender initiated the chase. Second, patrolled area was estimated by noting the position of the defender every 15 s on each of the three days (20x3=60 observations). I estimated the patrolled area using the 90% minimum-convex-polygon method (Schoener 1981). Intruder pressure was estimated as the average number of intruders over the patch in scan samples taken every 15 s. An intruder was considered to be in the patch when any part of its body overlapped it from the top view.

To test the assumption that benefits of defence increase with patch size, I quantified the percentage of available food and the number of food pellets eaten by the defender. With the exception of the 1-cell patch, all the food (1 or 2 pellets) in the cell was considered to be eaten by the first fish to feed in a cell. A feeding fish characteristically dipped head-down into a cell. On a few occasions a fish was immediately chased from a food cell after eating one of the two food pellets. It was usually impossible to determine the exact number of food pellets eaten by any fish in the 1-cell patch, which contained 9 pellets. Therefore, I noted the percentage of the total feeding time the defender spent in the patch and assumed it ate that percentage of food. The number of pellets eaten by the defender was calculated as a z-score (Snedecor & Cochran 1989) separately for (i) the first two replicates and (ii) the remaining replicates. Hence, I was able to compare the foraging success of all defenders despite the different maximum rations used in the two series of replicates.

I recorded the net benefits of defence by weighing both the intruders and defenders after the 10-day trial. Because there was variation in both defender and intruder size, I expressed change in weight as the mean percentage growth rate separately for defenders and intruders. My measure of net benefits was a z-score of the percentage growth rate to account for the two different maximum rations used in the experiment (see above).

I expressed patch size in two ways: patch radius (1, 3, 5, 7, 9, and 11) and patch area (1, 9, 25, 49, 81, and 121 cells). I used patch radius and patch area as the x-axis when analyzing the defender's chase radius and patrolled area, respectively. This allowed me to compare the independent variables to the actual radius and area of the patch, respectively. When testing for linear or quadratic relationships, all independent variables were analyzed with respect to both patch radius and area. The qualitative shapes of curves or tests of significance were not affected by the choice of x-axis. Hence, in my thesis I always present the analysis with the higher R^2 value.

Results

Because there were no significant differences in behaviour between Days 7 and 9 (Paired *t*-tests: all probabilities >0.05), I combined the data for all three days. Mean time to eat all the food in the patch increased significantly (Linear regression: $F_{1,30}=52.67$, $R^2=0.64$, $P<0.0001$) with patch size ($\overline{X}=0.37$, 1.17, 2.24, 2.67, 3.19, 3.42 min for patch sizes 1, 3, 5, 7, 9, and 11, respectively), and was less than 5 min for all 96 trials. Hence, I analysed only the first 5 min of each feeding period. I used paired *t*-tests to determine if the behaviour of the defender or intruders changed after all the food was eaten, within the 5-min period. None of the rates of behaviour differed when food was present or absent (Paired *t*-tests, all probabilities >0.05) and were, therefore, combined and expressed per 5-min trial. Measurements of territory size, however, changed after all the food was eaten and, hence, were calculated for when food was present and absent.

Cost of defence versus patch size

A key assumption of my study is that the size of the defender's territory will approximate the size of the food patch. As assumed, territory size increased with patch size. Average chase radius when food was present and absent both increased with increasing patch radius (Fig. 5). The average chase radius increased after all the food was eaten (Paired *t*-test: $t_{30}=4.64$, $N=30$, $P<0.0001$). The average chase radius in the presence of food did not differ significantly from the actual patch radius (i.e. 95% C.I. overlapped the solid line in Fig. 5), except for patch size 11. In the absence of food, average chase radius was significantly larger than the actual patch radius for patch sizes 1, 3, and 5 and not significantly different from the actual patch radius for patch size 7, 9, and 11. The decline in both chase radii relative to the actual patch radius for large patch sizes is likely due to the space constraints of the aquaria. Likewise, the average patrolled area increased with increasing patch area (Fig. 6). The average patrolled area differed significantly from the actual patch area (i.e. 95% C.I. did not overlap the solid line in Fig. 6) for patch area 49, 81, and 121; the patrolled area was far less than the actual patch area. The decline in patrolled area relative to the actual patch area for the three large patch areas was again likely due to the space constraints of the aquaria

Two measures of the costs of defence, chase rate and the number of intruders in the patch, both increased linearly with increasing patch radius (Figs. 7 and 8). The expected number of intruders over the patch was calculated, based on the size of the patch relative to the aquarium. Interestingly, the average number of intruders in the patch did not differ significantly from the number expected by chance (i.e. 95% C.I. overlapped the dashed line in Fig. 8). Chase rate and intruder pressure also increased linearly with increasing patch area, but the relationship was stronger (i.e. a higher R^2 value) when plotted against patch radius rather than patch area.

Benefits of defence versus patch size

The percentage of food eaten by the defender decreased significantly as patch size increased (Fig. 9). I calculated the expected value of the defender's share by dividing the total amount of food in the patch by the average total number of fish in the patch at any one time. The defender's share did not differ significantly from the expected percentage (i.e. 95% C.I. overlapped the dashed line in Fig. 9) for all patch sizes, with the exception of patch size 1 and 11, where they ate a smaller and larger percentage, respectively.

The number of pellets eaten by the defender increased significantly and asymptotically as patch size increased (Fig. 10). As expected, the growth rate of the defender increased with the number of pellets eaten (Fig. 11).

Net benefits of defence versus patch size

Growth rate of the defender first increased and then decreased with increasing patch size (Fig. 12); growth rate appeared to be highest on patch size 7 (patch area=49 cells). A planned comparison (Hintze 1995) showed that growth rate was significantly higher in patch size 7 than in patch size 1 (t=3.38, P=0.002) and higher in patch size 7 than in patch size 121 (t=2.05, P=0.05). Average intruder growth rate similarly first increased and then levelled off with increasing patch radius (Fig. 13).

Correlates of defender success

Patch area explained 55% of the variation in the number of pellets eaten by defenders (Fig. 10). To test the hypothesis that the residual variation in defender foraging success was related to its effectiveness of defence, I correlated the residuals from the quadratic regression of Fig. 10 with the residual variation in chase radius in the presence of food (Fig. 5), chase rate (Fig. 7), and number of intruders (Fig. 8). The relative foraging success of the defenders increased as their relative chase radius increased (Fig. 14a) and decreased as relative chase rate (Fig. 14b) and intruder pressure (Fig. 14c) increased. However, all three factors were inter-related. Intruder pressure was positively correlated with chase rate (Spearman rank correlation: r_s=0.38, N=32, P=0.03) and negatively correlated with chase radius in the presence of food (Fig. 15). A multiple regression analysis showed that the foraging success of the defender increased significantly (t=3.09, P=0.005) as relative chase radius increased and decreased significantly (t=2.29, P=0.03) as relative chase rate increased (Y=-0.15(chase rate) + 0.12(chase radius) + 0.06; $F_{2,27}$=11.32, R^2=0.46, P<0.0001). Intruder pressure was omitted from the multiple regression due to its correlation with both chase rate and chase radius.

Defender growth rate increased significantly with the number of pellets eaten (Fig. 11). To test what other factors might have influenced defender growth rate, I correlated the residuals from the least squares regression in Fig. 11 with the residual variation from Figs. 5, 7, and 8. Defender growth rate decreased significantly with increasing intruder pressure (Fig. 16).

Discussion

Defended area versus food patch size

Chase radius when food was present provided strong support for the key assumption that the dominant fish will defend a territory similar in size to the food patch. Interestingly, the fish expanded their territory after all food had been eaten. The defenders were perhaps responding to the decline in food abundance by expanding their territory size as has been observed in other taxa (e.g. in rainbow trout, Slaney & Northcote 1974; iguanid lizards, Simon 1975; rufous hummingbirds, Gass et al. 1976, Kodric-Brown & Brown 1978; nuthatches, Enoksson & Nilsson 1983; and caddisflies, Hart 1985). Alternatively, when the food is depleted, the defender may be "freer" to leave the patch because it does not have to worry about finding food or preventing intruders from stealing food. Hence, defenders may have been increasing their "short-term" territory size to intimidate intruders from stealing food during the next feeding period.

The patrolled area differed from the actual patch area more than did the chase radius in the presence of food. This difference may have been partly because patrolled area was not measured separately when food was present and absent. Therefore, the patrolled area may be larger than the patch because defenders expanded their territory when food was depleted. This suggestion cannot explain, however, why the patrolled area was smaller than the patch for patch areas 49, 81, and 121. The difference between the two measures of space use suggests that defenders concentrated their feeding in the centre of the patch, but chased intruders as they entered the patch.

Costs and benefits of defence versus patch size

Two measures of the cost of defence, chase rate and number of intruders on the patch, supported the assumption that the costs of defence increase with territory size. Chase rate (Tricas 1989) and the number of intruders increase with increasing territory size (Wittenberger 1981; Davies & Houston 1984). Interestingly, the average number of intruders in the patch did not differ significantly from the number expected by chance based on the area of the food patch. This result might seem to imply either that the intruders were not attracted to the patch or that defenders were not very effective at excluding them. The first suggestion does not seem reasonable because intruders waited at the edge of the food tray until the lid was removed and then darted into the patch. Secondly, only the active chasing by the defender kept the number of intruders below four. Hence, the fact that the number of intruders in the patch did not differ from the random expectation was probably a coincidental result of the opposing forces of intruders being attracted to the patch and defenders expelling intruders from the patch.

The defender's chase rate increased at a slower rate than did the number of intruders with increasing patch size. This result suggests that the defender chased a smaller percentage of intruders and was less able to defend an exclusive area as patch size increased. Our data supports Wittenberger's (1981) prediction that exclusivity of defence declines with increasing territory size.

Cost curves are generally expected to increase either linearly or in a decelerating way with territory area (Schoener 1983). Both of my cost curves increased linearly with patch radius and patch area. However, the slightly stronger relationship between costs of defence and patch radius, rather than patch area, suggests that the costs of defence increased with territory area somewhere between an exponent of 0.5 and 1.0 (i.e. costs $\propto$ area$^{0.5\text{-}1.0}$). Costs did not increase in an accelerating way with territory area in my study, as is occasionally suggested in the literature (e.g. Fig. 1; Ebersole 1980), probably because the total number of intruders was held constant. An accelerating cost curve may require that more intruders be attracted to larger territories (Schoener 1983).

As expected, the number of pellets eaten by the defender initially increased with increasing patch size and then levelled off (Fig. 10). The decelerating benefit curve was caused by the experimental design (i.e. Fig. 4) and the fact that defenders ate a smaller percentage of food as patch size increased (Fig. 9). The effectiveness of territoriality as a foraging strategy can be evaluated by comparing the defender's share to the 20% expected if the defender was but one of five equal competitors exploiting the patch. Defenders ate significantly more than 20% of the food on all patch sizes (*t*-tests: all probabilities <0.05) with the exception of patch size 5 (*t*-test: $t_5=1.331$, $P=0.26$). The defender's share of the food for patch sizes 3-11 was accurately predicted by the number of intruders on the patch (i.e. 95% C.I. overlapped the dashed line in Fig. 9). Even though there was only an average of 0.2 intruders in the food patch for patch size 1, the defender ate far less than expected. This result can be explained because intruders entered the food patch first in

80% of the 15 trials. The first intruder ate a minimum of two of the nine pellets (i.e. 22% of the available food) in the patch. In contrast, two pellets represents only 2% on patch size 11. The results for patch sizes 3 to 11 suggest that once in a patch intruders are as efficient as defenders at foraging. In my study, the primary benefit of defence appeared to be a reduction in the number of competitors in the patch.

Correlates of defender success

After taking patch area into account, the number of pellets eaten by the defender decreased with increasing chase rate and number of intruders. An increase in the number of intruders suggests more food stolen and more chasing by the defender. This interpretation is supported by the fact that both chase rate and intruder pressure were positively correlated. Defenders with a large relative chase radius also ate more food. A larger chase radius might indicate an effective defender or ineffective intruders. This interpretation is supported by the negative correlation observed between intruder pressure and chase radius (Fig. 15). This inverse relation between intruder pressure and territory size supports a key prediction of the optimal territory size model (Fig. 1c). In summary, the foraging success of defenders increased in a decelerating manner with patch size, increased with relative chase radius and decreased with relative chase rate.

The number of pellets eaten was the best predictor of the growth rate of the defender. However, an increase in intruder pressure was associated with a decrease in growth rate, independent of the number of pellets eaten. This result cannot be explained by defenders spending too much energy chasing intruders because chase rate had no independent effect on the growth rate of the defender. Perhaps the presence of the intruders acts as a social stress causing a decreased growth efficiency. Previous studies have shown that "social stress" might cause reduced appetite (Arctic charr Salvelinus alpinus, Jobling & Wandsvik 1983) and reduced growth efficiency (blennies Blennius pholis, Wirtz 1975, Wirtz & Davenport 1976; steelhead trout Oncorhynchus mykiss, Abbott & Dill 1989). The latter seems to apply best to my results. Defenders with more intruders on their territory gained less weight, perhaps because the social stress caused by intruders contributed to a decrease in their growth rate.

General implications

Because I was able to manipulate territory size effectively, my study provides one of the strongest tests of the assumptions and predictions of the simple optimal territory size model. As is generally assumed, the benefits of defence increased in a decelerating manner with increasing territory size and costs of defence increased linearly with an increase in territory size (Fig. 17a).

Growth rate, a measure of the net benefits of defence, initially increased with territory size, peaked at a patch size of 7, and then decreased (Fig. 17b). Until now, the best demonstration of a relationship between territory size and fitness was provided by Carpenter et al. (1983; Fig. 2). However, the growth rate of the hummingbirds was highest at an intermediate territory size for only one of five birds. The initial increase in growth rate with increasing territory size in my study was the result of more food eaten, as the simple optimality model assumes. The decrease in growth rate on very large territories is assumed to be the result of the increasing energetic costs of defence (Hixon 1980; Schoener 1983). My data do not support this assumption. Instead, the decline in growth rate of defenders seems to be the result of a decrease in growth efficiency caused by the "social stress" of intruders in the patch. Taken together, my study provides strong support for the assumptions and predictions of the simple optimal territory size model. In particular, my study provides the strongest support for the key prediction that fitness varies as a function of territory size and that fitness is highest on a territory of intermediate size.

In my study, the fish had no other choice about what size of patch to defend. An interesting follow-up experiment would allow defenders to choose the size of their territory. Presumably, defenders would choose a territory size that would maximize their growth rate. Carpenter et al. (1983) demonstrated this result in the field. Four of five hummingbirds adjusted their territories to a size that increased their growth rate. An experimental demonstration would provide even stronger evidence that animals can choose to defend an optimal territory size.

Table 1. The number, weight, and distribution of food pellets for all patch sizes

Patch area (no. of cells)	Total number of pellets	Weight of food (mg)	Total pellets/cell	Approximate distribution
1	9[1](9)	9[1](13)	9[1](9)	every cell
9	18(18)	17(26)	2(2)	every cell
25	25(50)	26(38)	1(2)	every cell
49	25(50)	32(48)	1(2)	every second cell
81	41(82)	34(51)	1(2)	every second cell
121	41(82)	36(54)	1(2)	every third cell

[1] In replicates 1 and 2 (or in replicates 3, 4, 5, and 6)

Figure 1. A simple model of optimal territory size. (a) As the territory increases, the costs, C, and the benefits, B, of defence increase. The animal should only defend a territory between a size of X and Y (where benefits > costs) and the maximum net benefit (benefit-cost) will be at a territory size A. (b) A decrease in the benefits of territoriality (B shifts to B^1) or a (c) decrease in the costs of territoriality (C shifts to C^1) both cause an increase in the optimal territory size from A to A^1 (after many authors, including Myers et al. 1981).

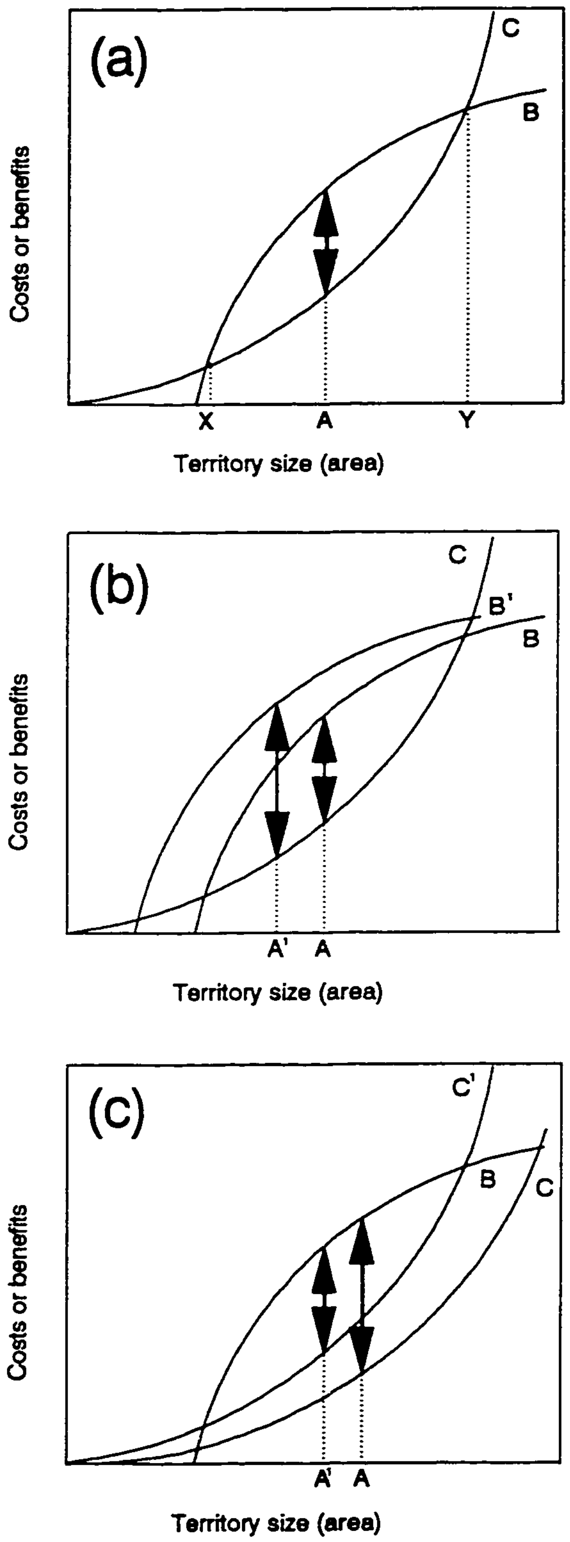

(a)
C
B
Costs or benefits
X
A
Y
Territory size (area)
(b)
C
B'
B
Costs or benefits
A'
A
Territory size (area)
(c)
C'
B
C
Costs or benefits
A'
A
Territory size (area)

Figure 2. The daily growth rate of one territorial rufous hummingbird plotted against territory size (number of flowers defended) for five successive days (numbers correspond to days). The bird started with a small territory on the first day, enlarged its territory on the third day and then gradually moved toward an intermediate size territory at which its daily growth rate was maximized (from Carpenter et al. 1983).

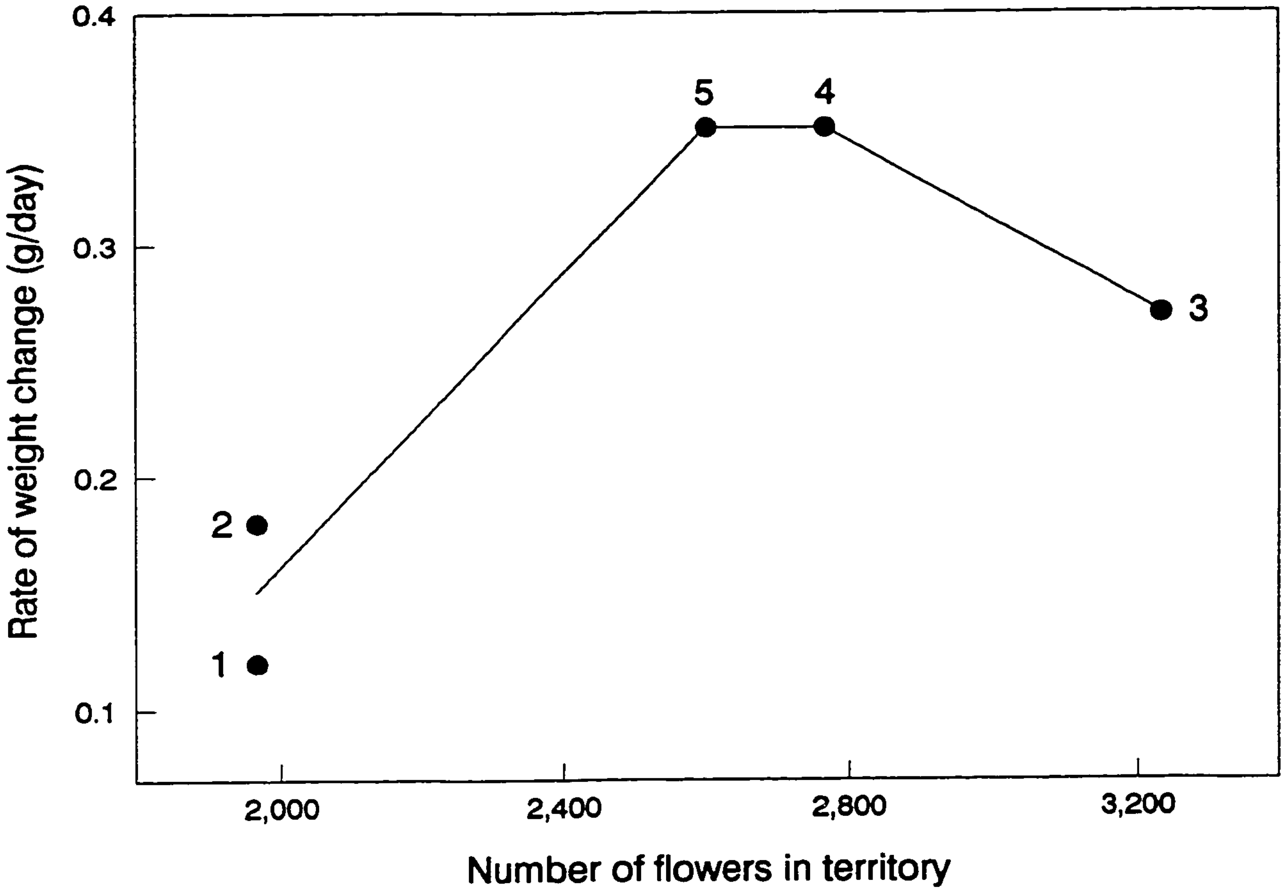
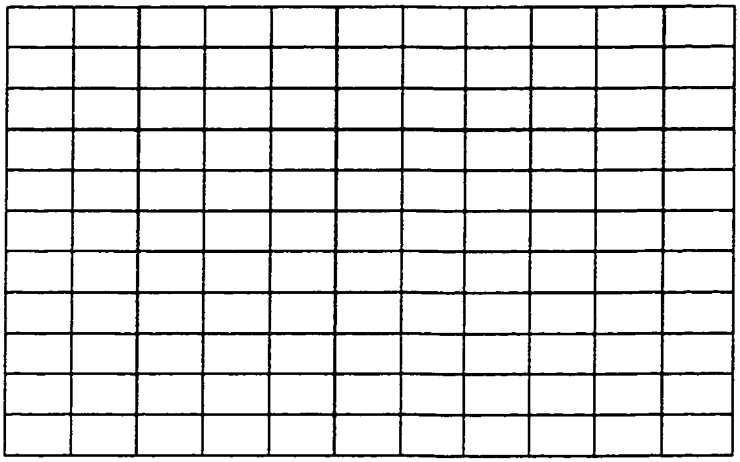
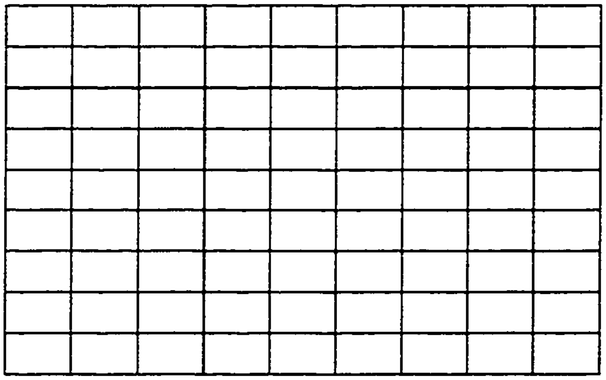

0.4
0.3
0.2
0.1
Rate of weight change (g/day)
5
4
3
2
1
2,000
2,400
2,800
3,200
Number of flowers in territory

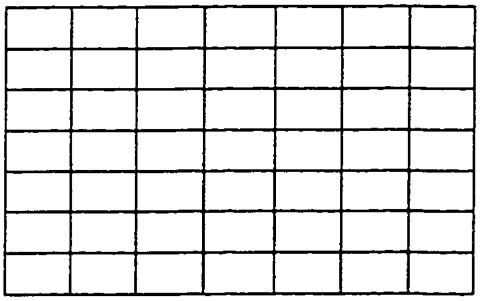
Figure 3. Food patch sizes. Patches, composed of the "cells" of plastic ice-cube trays, were of six sizes: 11 (11x11 cells), 9 (9x9 cells), 7 (7x7 cells), 5 (5x5 cells), 3 (3x3 cells), and 1 (1 cell).



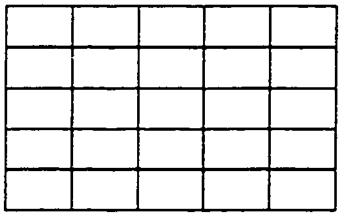
11



9



7



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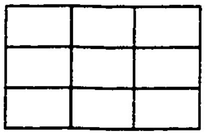


3

1

Figure 4. The percent of the maximum ration fed twice a day to fish exposed to six different patch sizes.

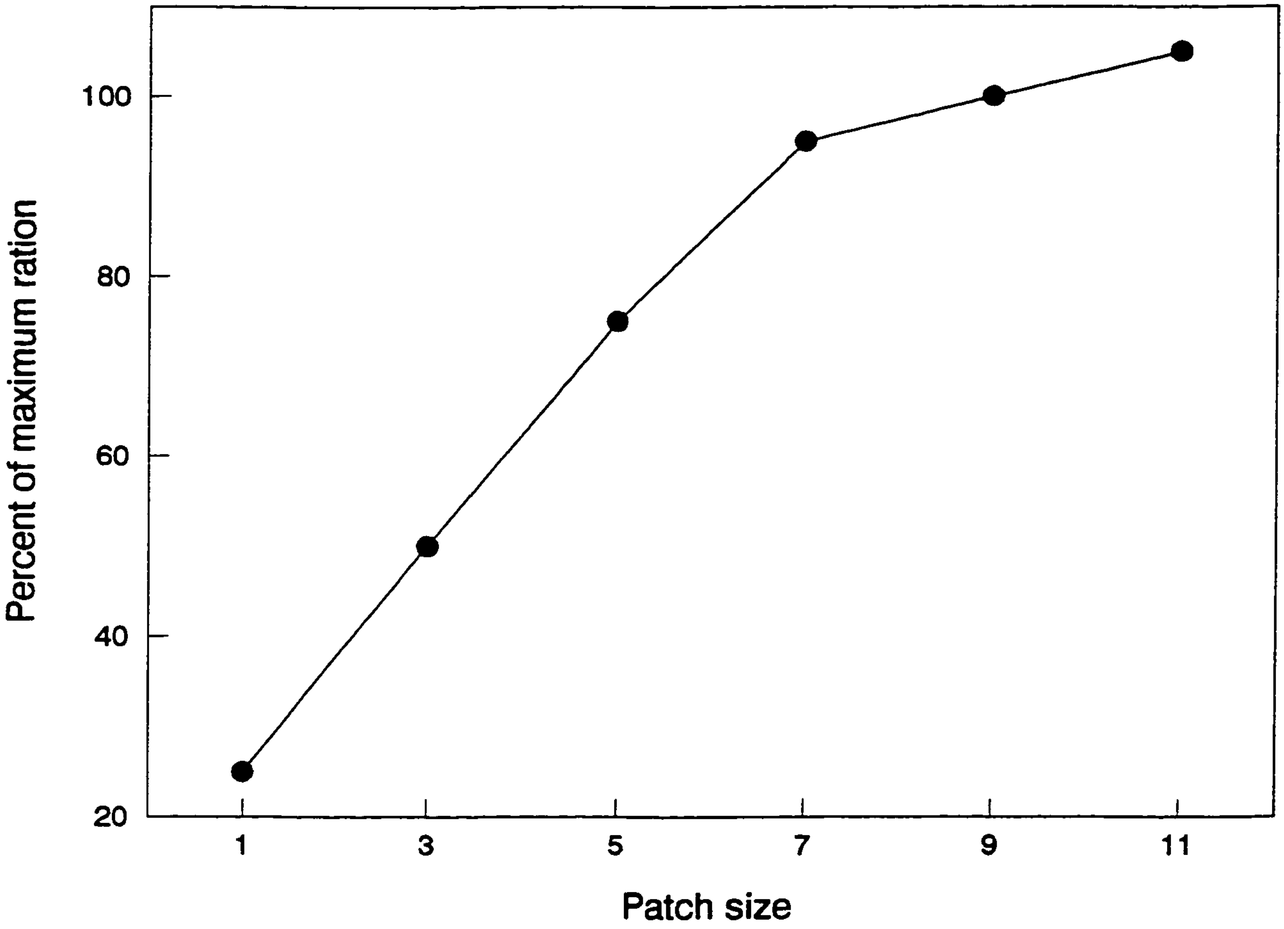

Percent of maximum ration
100
80
60
40
20
1
3
5
7
9
11
Patch size

Figure 5. Mean chase radius (±1 SE, N=4, 5, or 6) of the defender in relation to food patch size, both in the presence (●, dashed line is the quadratic regression: $Y=-0.13x^2+3.40x-1.48$, $F_{2,27}=75.67$, $R^2=0.85$, $P<0.0001$) and absence (○, dotted line is the least-squares regression: $Y=0.68x+14.07$, $F_{1,30}=7.26$, $R^2=0.20$, $P=0.011$) of food. The solid line represents the actual average patch radius ([length + width]/4). For clarity of presentation, points for patch radius 5, 7, 9, and 11 are staggered.

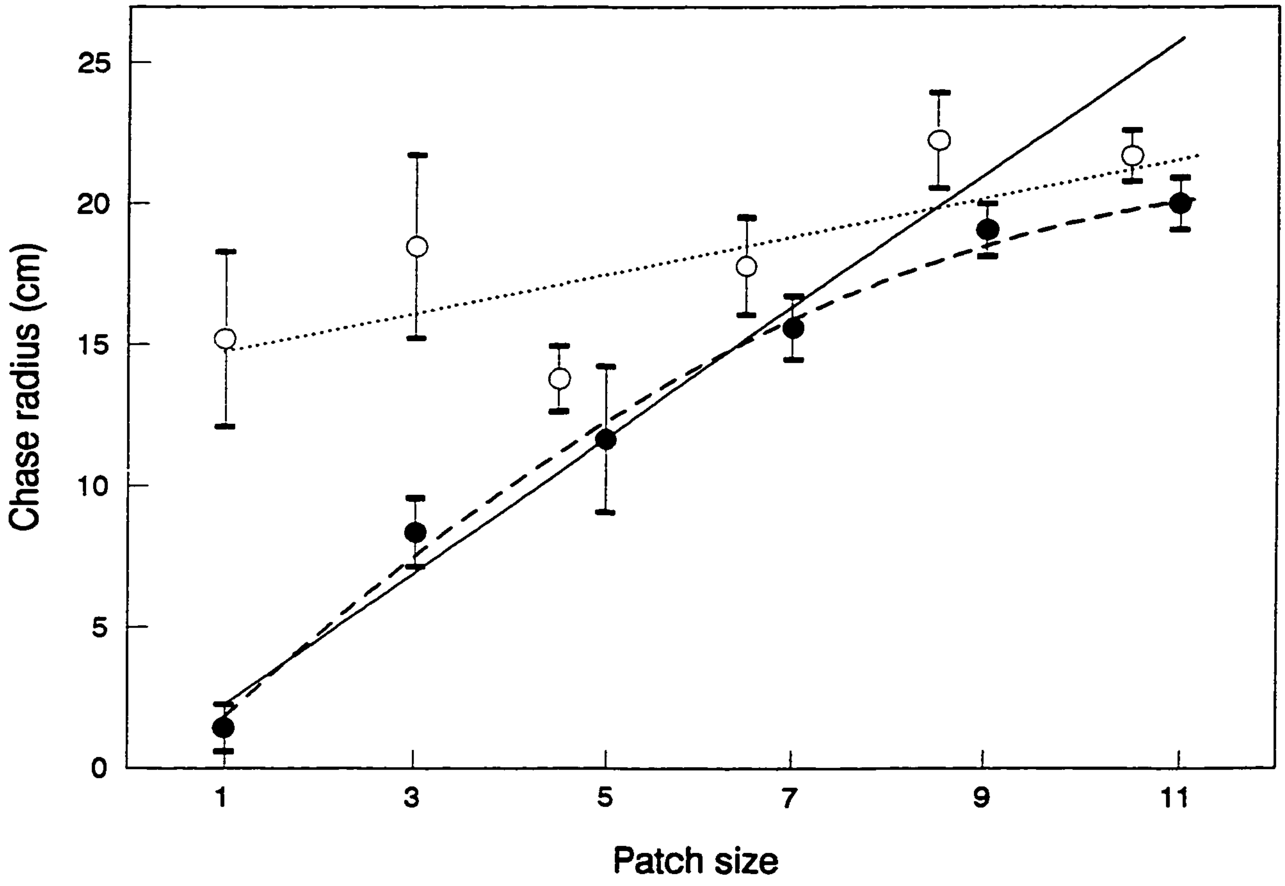

Chase radius (cm)
0
5
10
15
20
25
Patch size
1
3
5
7
9
11

Figure 6. Mean patrolled area (±1 SE, N=5 or 6) of the defender in relation to food patch area. Patrolled area was estimated by noting the position of the defender every 15 s (20 points) on each of the three days. The patrolled area was then estimated using the 90% minimum-convex-polygon method (Schoener 1981). The data were heteroscedastic; the dotted line, representing the least squares regression (Y=10.24x+452.15), was fitted for visual purposes only. There was a significant correlation between patch area and patrolled area (Spearman rank correlation: r_s=0.67, N=32, P<0.0001). The solid line represents the actual patch area.

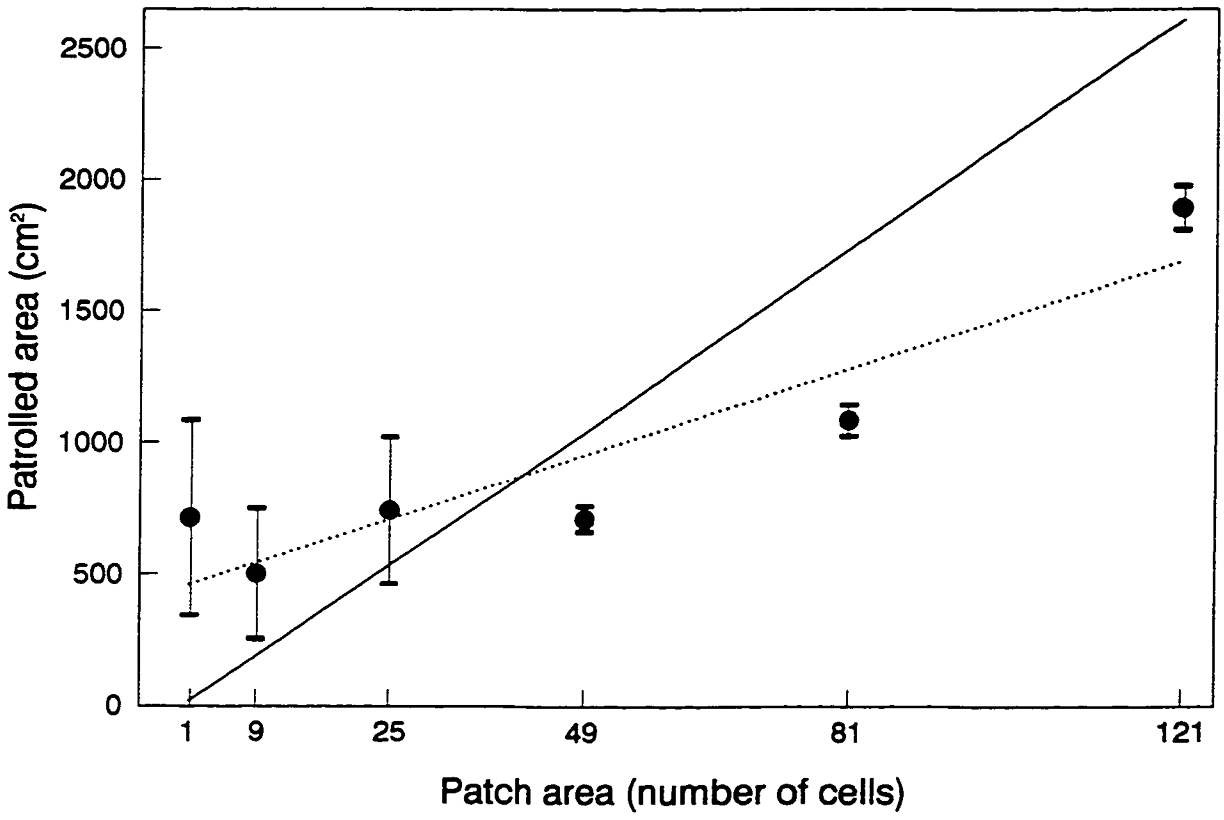

Patrolled area (cm²)
2500
2000
1500
1000
500
0
1
9
25
49
81
121
Patch area (number of cells)

Figure 7. The effect of food patch size on mean (±1 SE, N=5 or 6) defender chase rate. The solid line represents the least squares regression: Y=0.18x+2.60 ($F_{1,30}$=5.30, R^2=0.15, P=0.028).

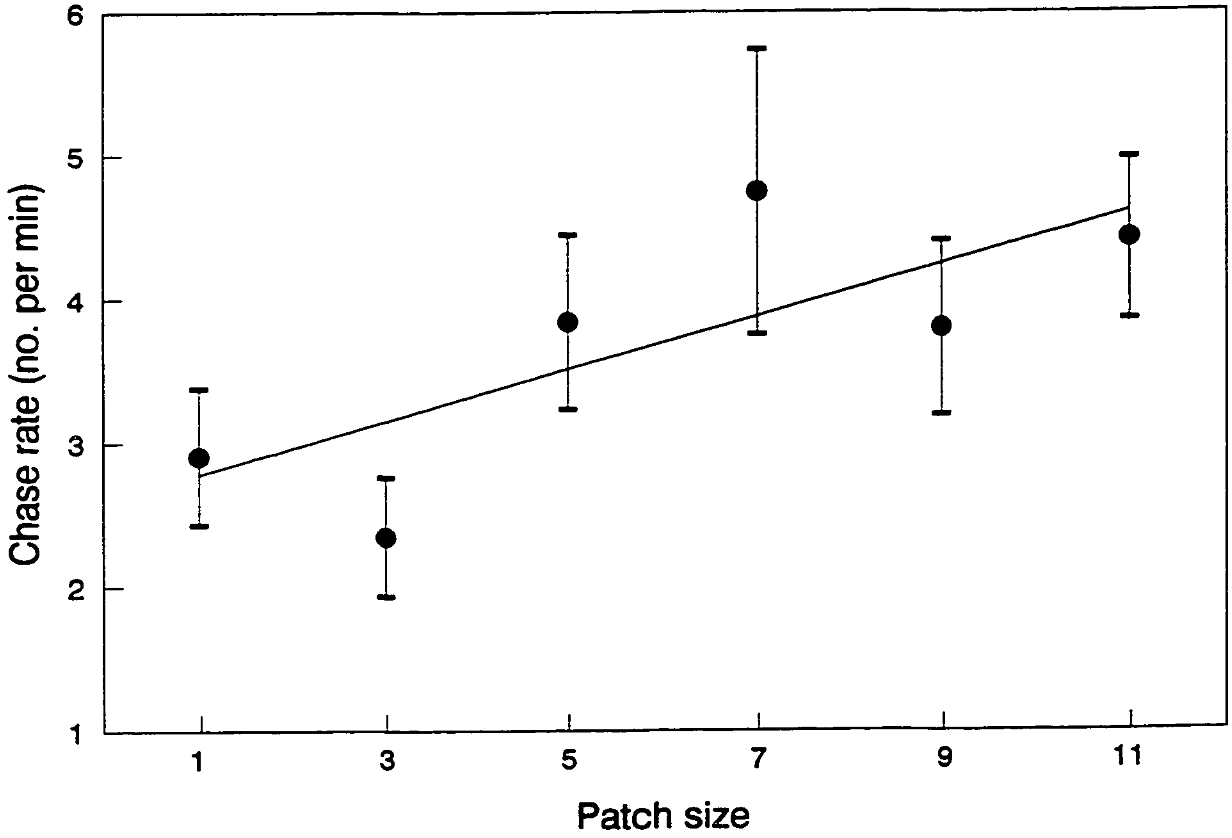
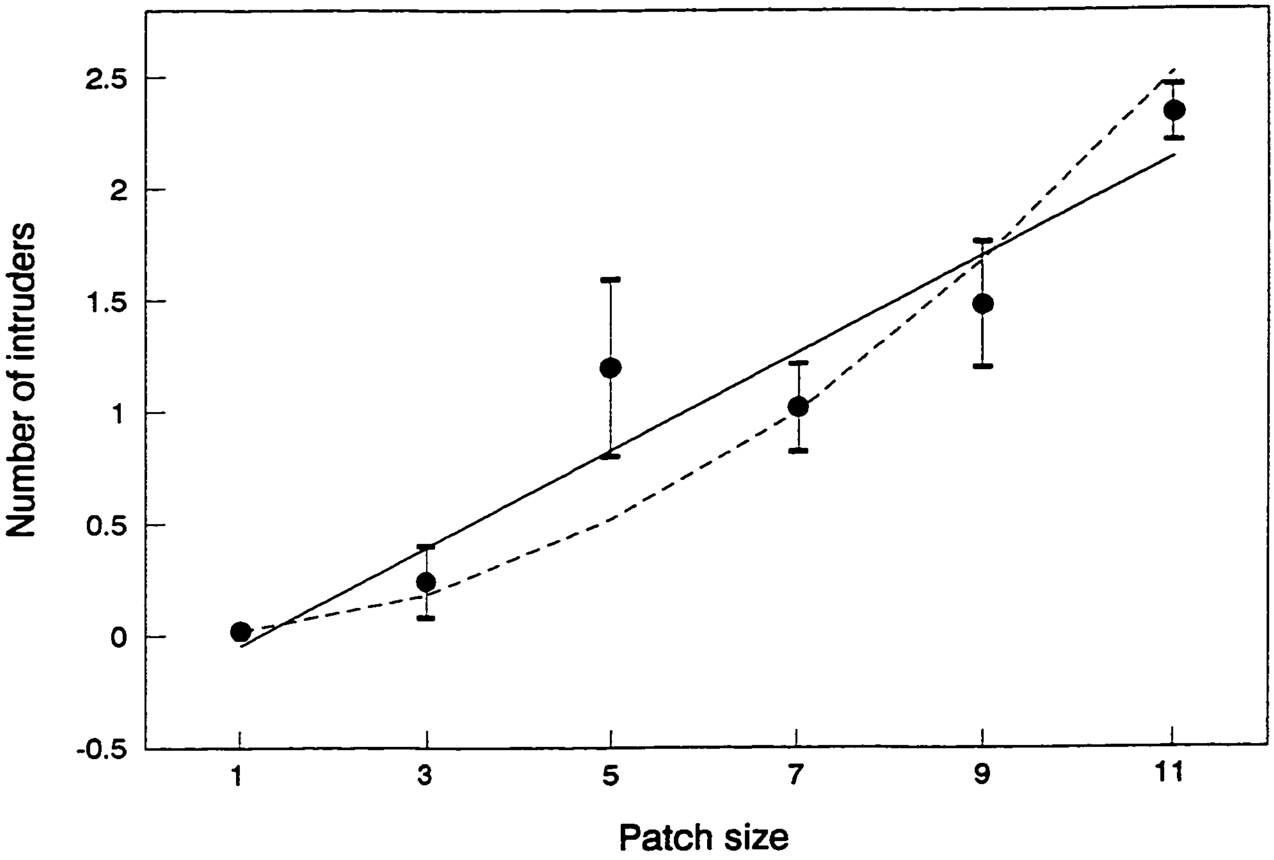
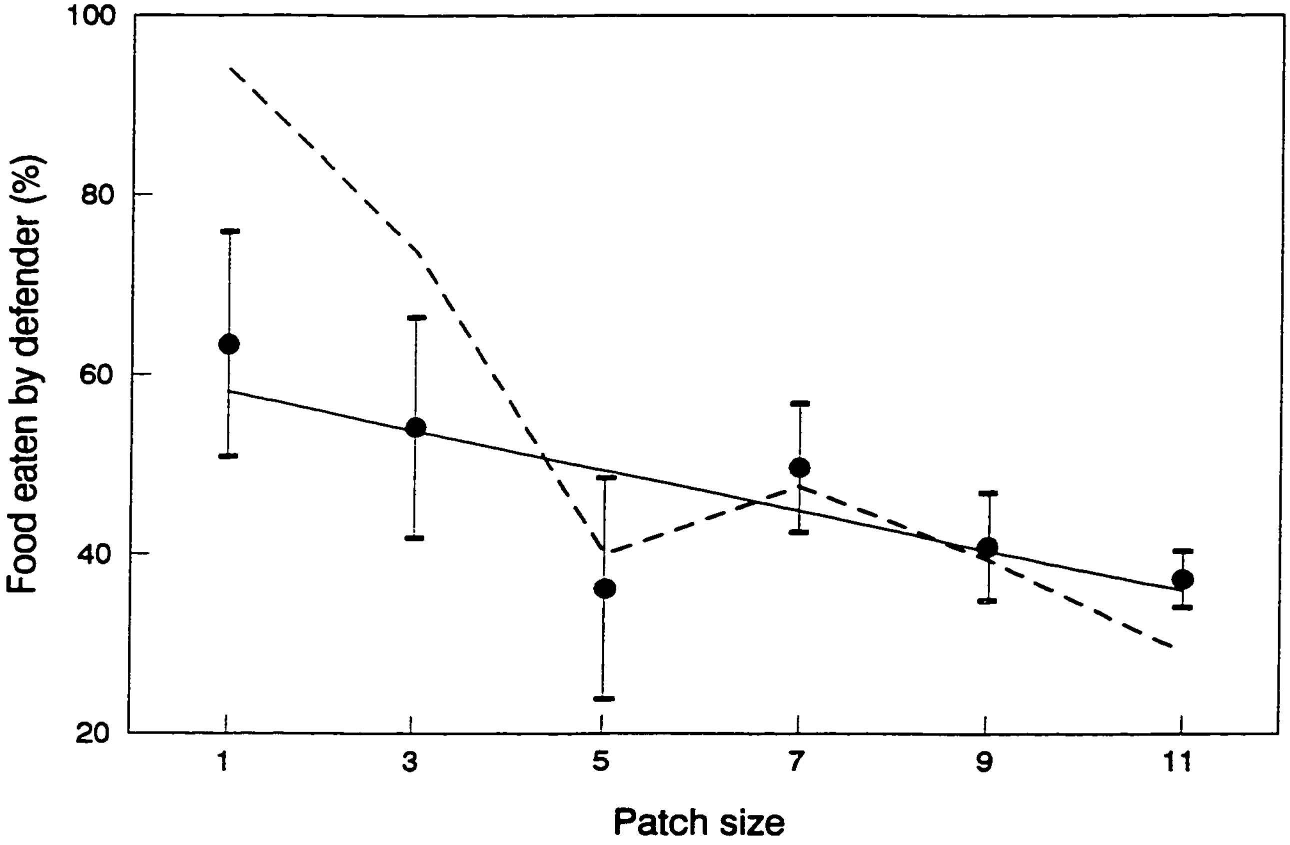

6
5
4
3
2
1
Chase rate (no. per min)
1
3
5
7
9
11
Patch size

Figure 8. Effect of food patch size on mean intruder rate, estimated as the mean (±1 SE, N=5 or 6) number of intruders over the patch in scan samples taken every 15 s. The solid line is the least squares regression: Y=0.22x-0.26 ($F_{1,30}$=62.77, R^2=0.68, P<0.0001). The dashed line represents the expected number of intruders over the patch based on the size of the patch relative to the aquarium.



Number of intruders
2.5
2
1.5
1
0.5
0
-0.5
1
3
5
7
9
11
Patch size

Figure 9. Effect of food patch size on the mean (±1 SE, N=5 or 6) percent food eaten by the defender. The solid line is the least square regression: Y=-2.21x+60.33 ($F_{1,30}$=4.28, R^2=0.13, P=0.047). The dashed line represents the expected percentage of food eaten by the defenders if the food is divided evenly among the defender and the average number of intruders in the patch.



Food eaten by defender (%)
100
80
60
40
20
1
3
5
7
9
11
Patch size

Figure 10. Effect of food patch area on the mean (±1 SE, N=5 or 6) number of food pellets eaten by the defender. The number of pellets eaten are expressed as a z-score to control for the two different maximum rations presented to the fish (see Table 1). The solid line represents the quadratic regression: $Y=-2.25*10^{-4}x^2+0.04x-1.14$ ($F_{2,29}=17.53$, $R^2=0.55$, $P<0.0001$).

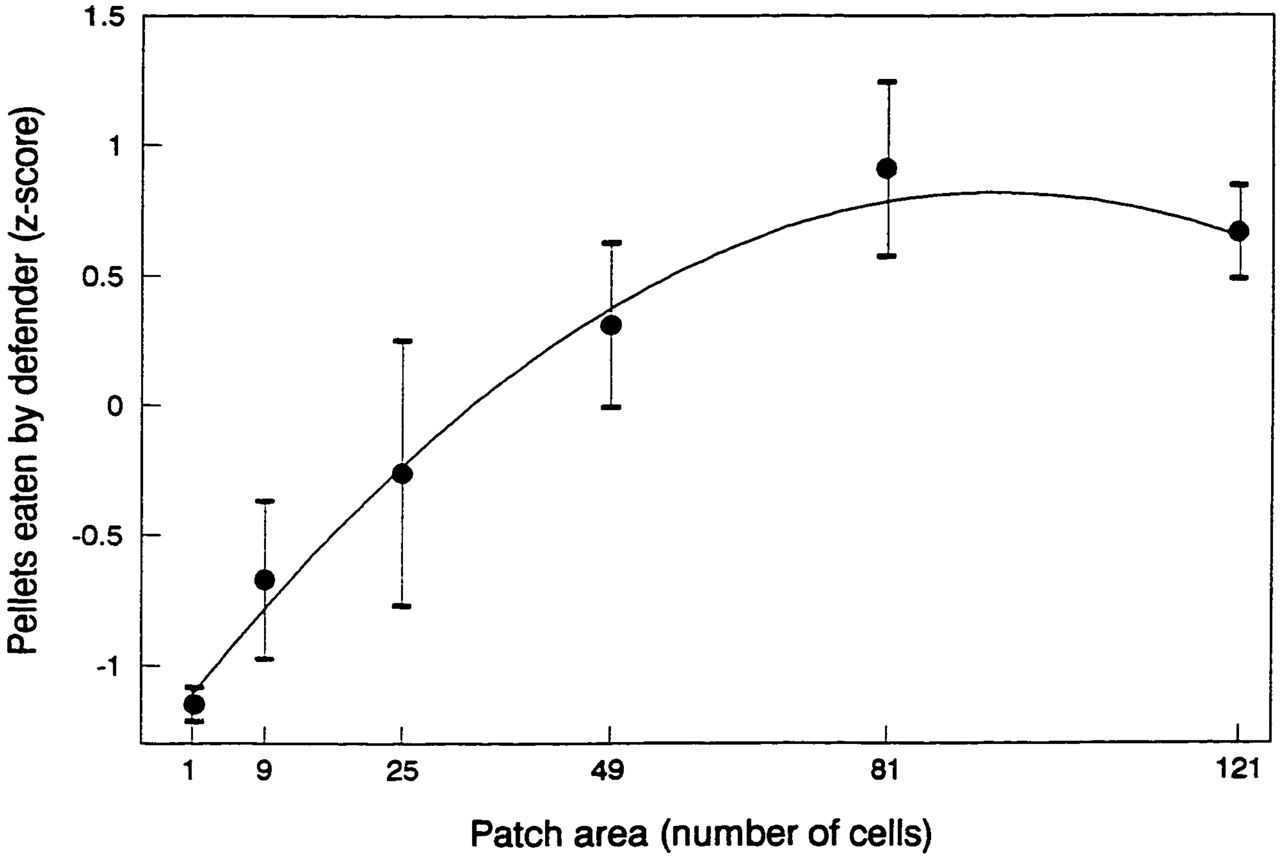

1.5
1
0.5
0
-0.5
-1
Pellets eaten by defender (z-score)
1
9
25
49
81
121
Patch area (number of cells)

Figure 11. Relationship between number of pellets eaten and the mean defender growth rate. Both axes were expressed as z-scores because of the two different rations used (see Table 1). The solid line represents the least squares regression: $Y=0.71x+22.02*10^{-7}$ ($F_{1,30}=30.79$, $R^2=0.51$, $P<0.0001$).

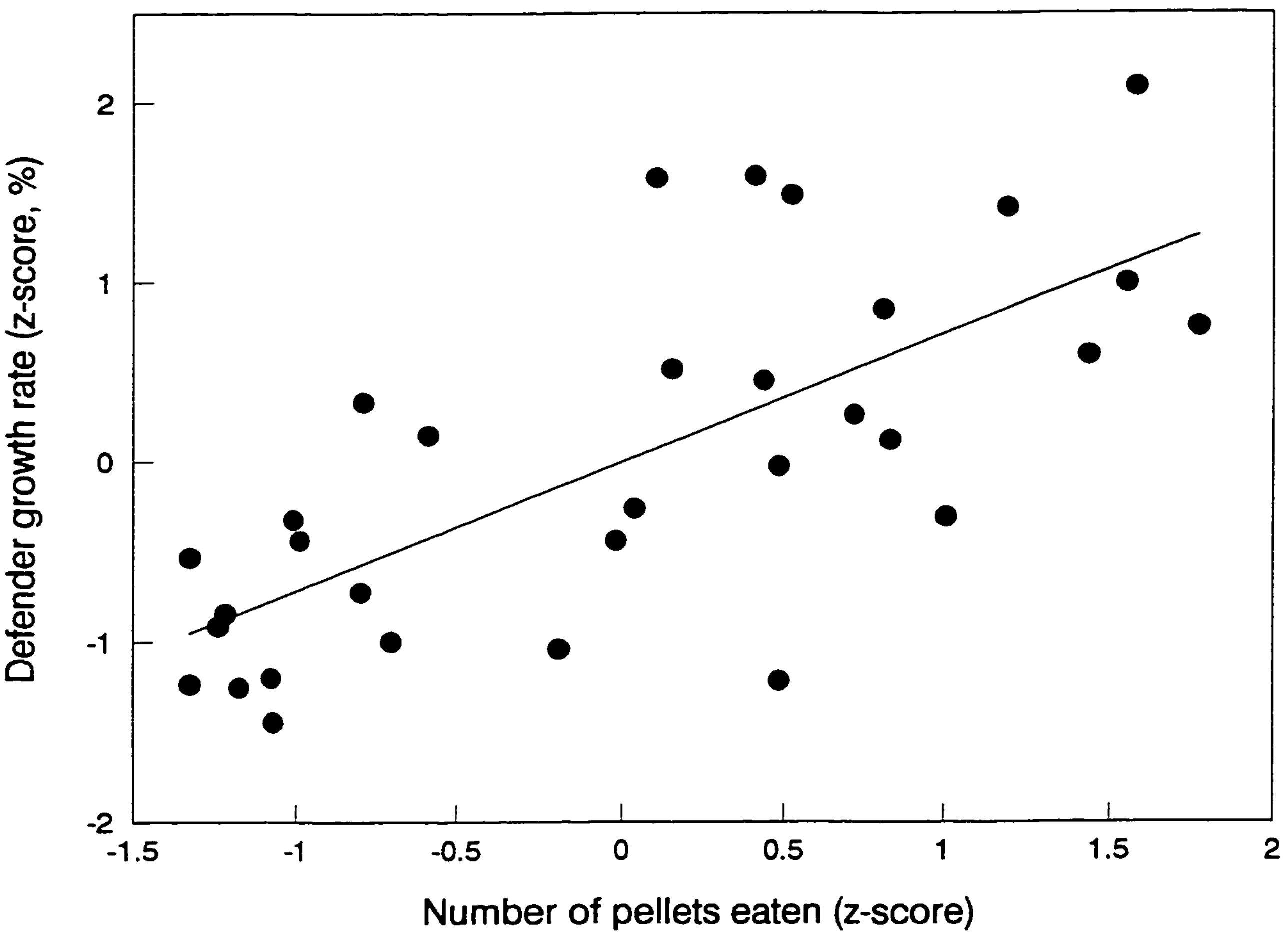

Defender growth rate (z-score, %)
2
1
0
-1
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
Number of pellets eaten (z-score)

Figure 12. Effect of patch area on mean (±1 SE, N=5 or 6) percent defender growth rate (z-score). Growth rate is expressed as a z-score to control for the two different maximum rations presented to the fish (see Table 1). The solid line represents the quadratic regression: $Y=-2.95*10^{-4}x^2+0.04x-0.77$ ($F_{2,29}=4.56$, $R^2=0.24$, $P=0.019$).

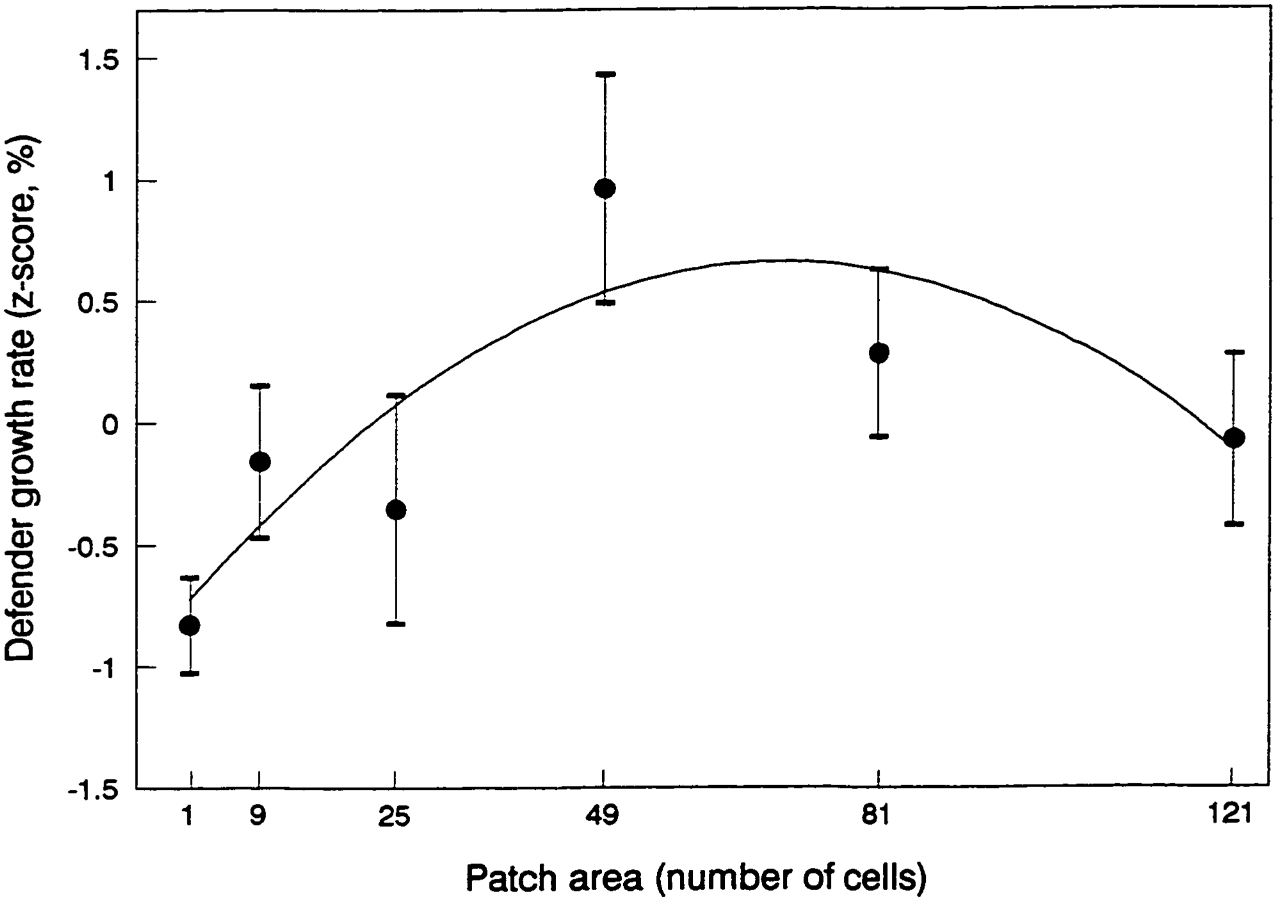
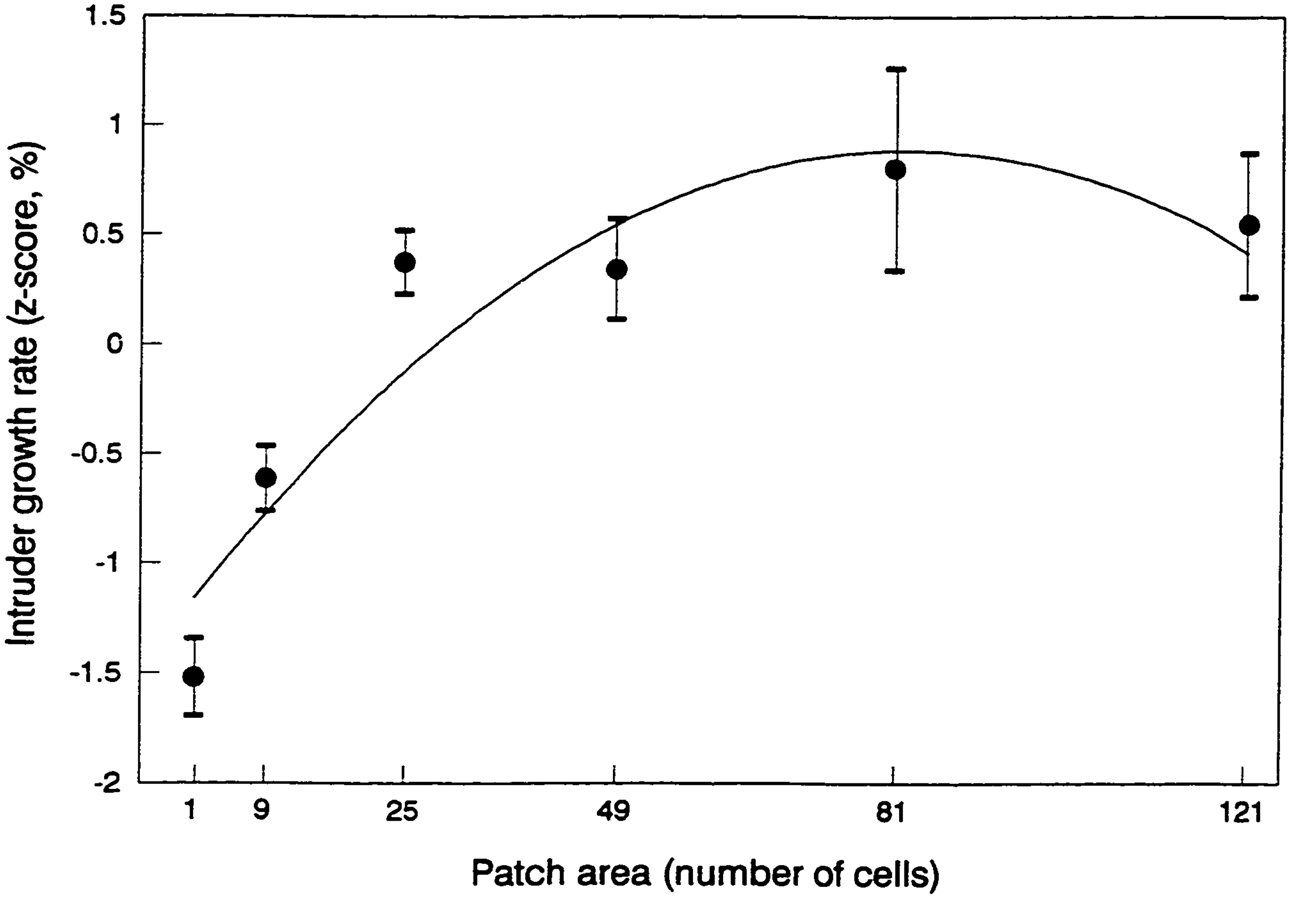

Defender growth rate (z-score, %)
1.5
1
0.5
0
-0.5
-1
-1.5
1
9
25
49
81
121
Patch area (number of cells)

Figure 13. Effect of patch area on mean (±1 SE, *N*=5 or 6) percent intruder growth rate. The solid line represents the quadratic regression: $Y=-3.11*10^{-4}x^2+0.51x-1.21$ ($F_{2,28}=19.69$, $R^2=0.58$, $P<0.0001$).



1.5
1
0.5
0
-0.5
-1
-1.5
-2
Intruder growth rate (z-score, %)
1
9
25
49
81
121
Patch area (number of cells)

Figure 14. Relative foraging success of defenders (residuals from Fig. 10) in relation to (a) relative chase radius in the presence of food (residuals from Fig. 5; Spearman rank correlation: r_s=0.50, N=30, P=0.005), (b) relative chase rate (residuals from Fig. 7; Spearman rank correlation: r_s=-0.48, N=32, P=0.006), and (c) relative number of intruders (residuals from Fig. 8; Spearman rank correlation: r_s=-0.55, N=32, P=0.001).

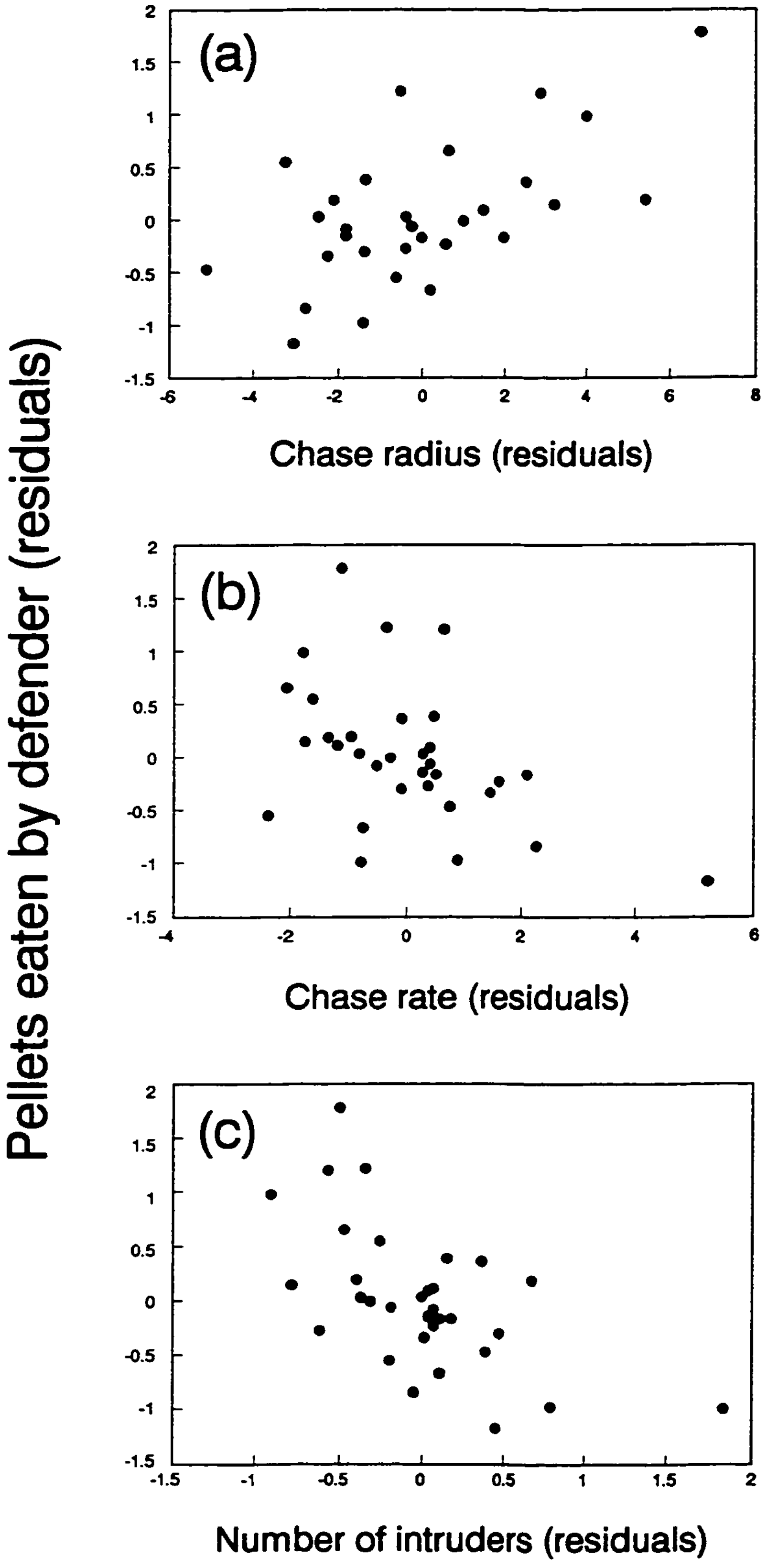
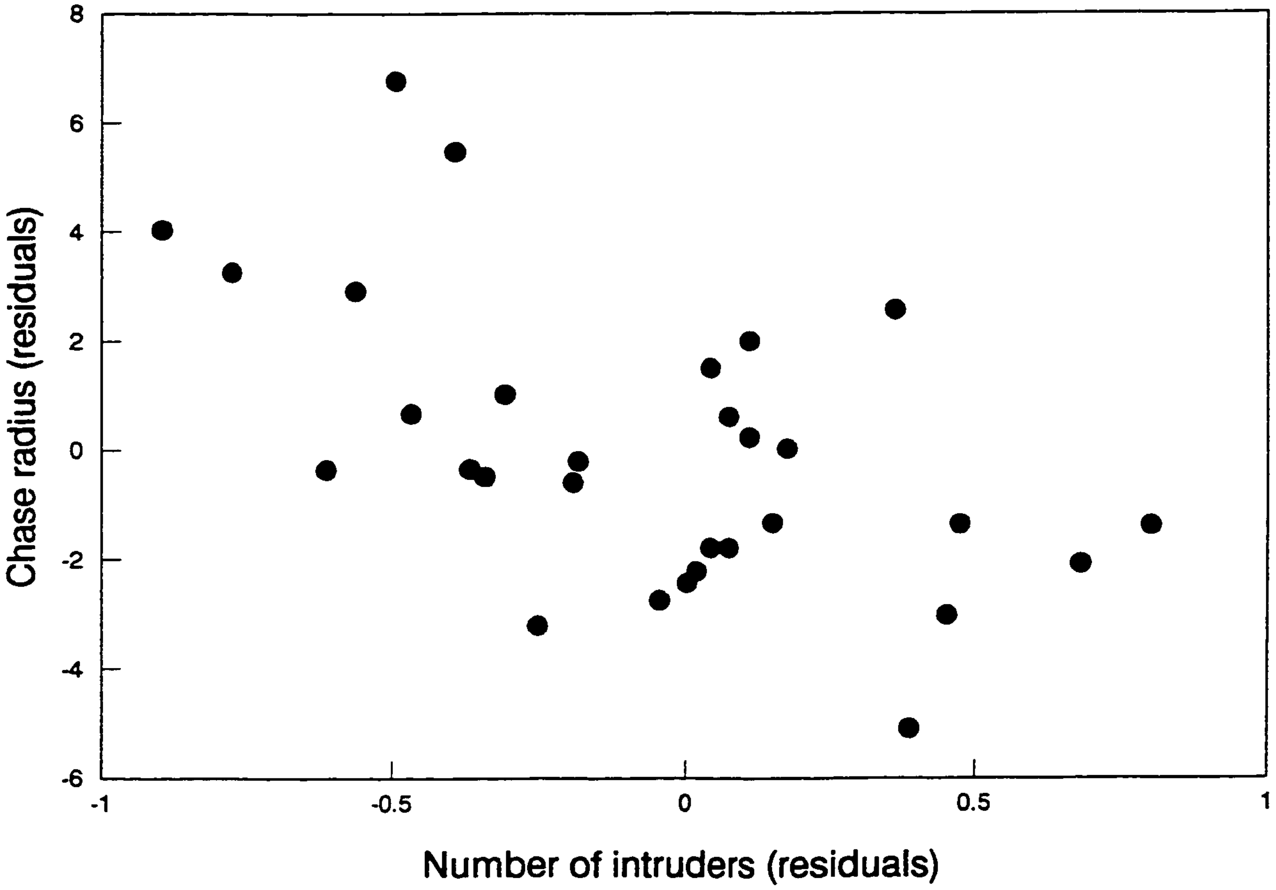

Pellets eaten by defender (residuals)
(a)
2
1.5
1
0.5
0
-0.5
-1
-1.5
-6
-4
-2
0
2
4
6
8
Chase radius (residuals)
(b)
2
1.5
1
0.5
0
-0.5
-1
-1.5
-4
-2
0
2
4
6
Chase rate (residuals)
(c)
2
1.5
1
0.5
0
-0.5
-1
-1.5
-1.5
-1
-0.5
0
0.5
1
1.5
2
Number of intruders (residuals)

Figure 15. Relative chase radius in the presence of food (residuals from Fig. 5) in relation to relative intruder pressure (residuals from Fig. 8; Spearman rank correlation: r_s=-0.50, N=30, P=0.005).



8
6
4
2
0
-2
-4
-6
Chase radius (residuals)
-1
-0.5
0
0.5
1
Number of intruders (residuals)

Figure 16. Relative defender growth rate (residuals from Fig. 11) in relation to relative intruder pressure (residuals from Fig. 8; Spearman rank correlation: r_s=-0.50, N=32, P=0.004).

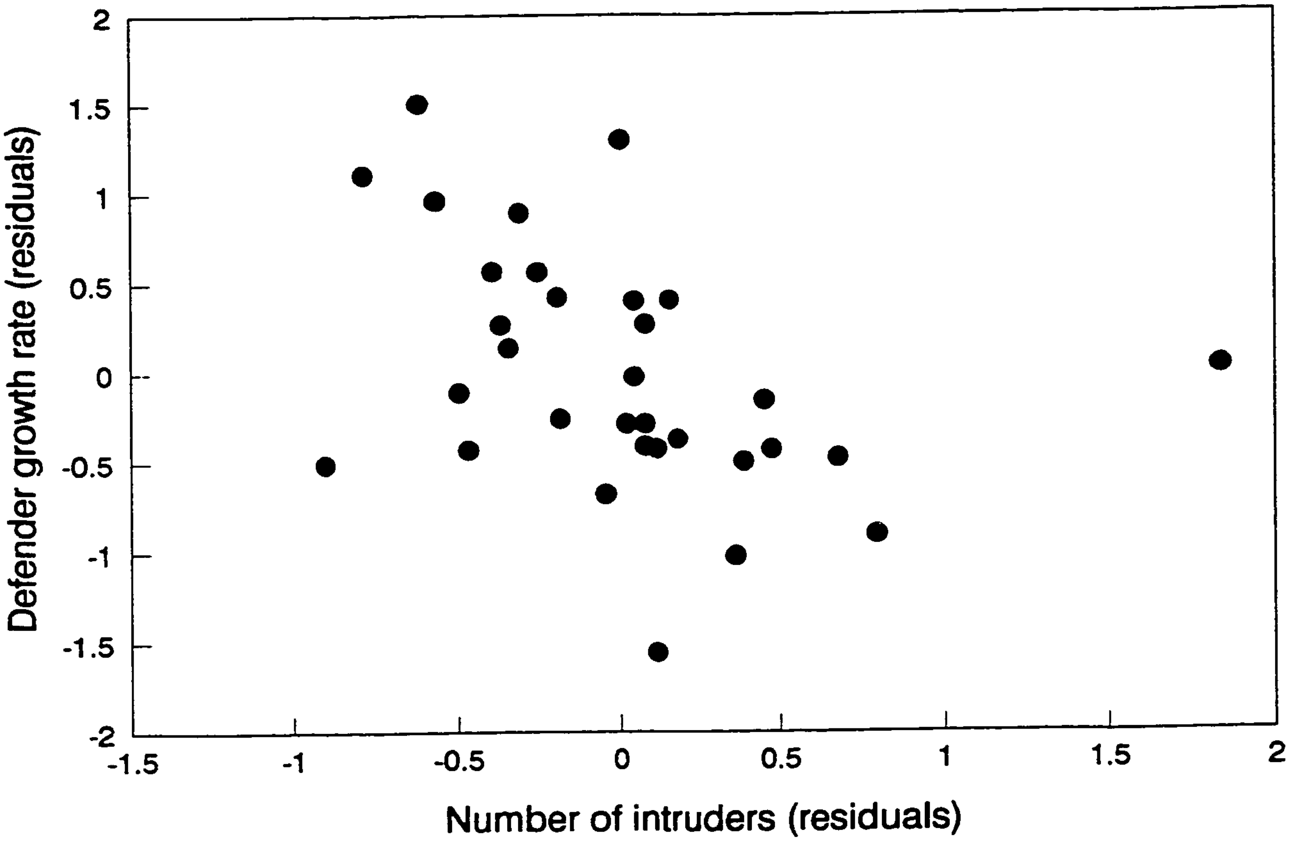
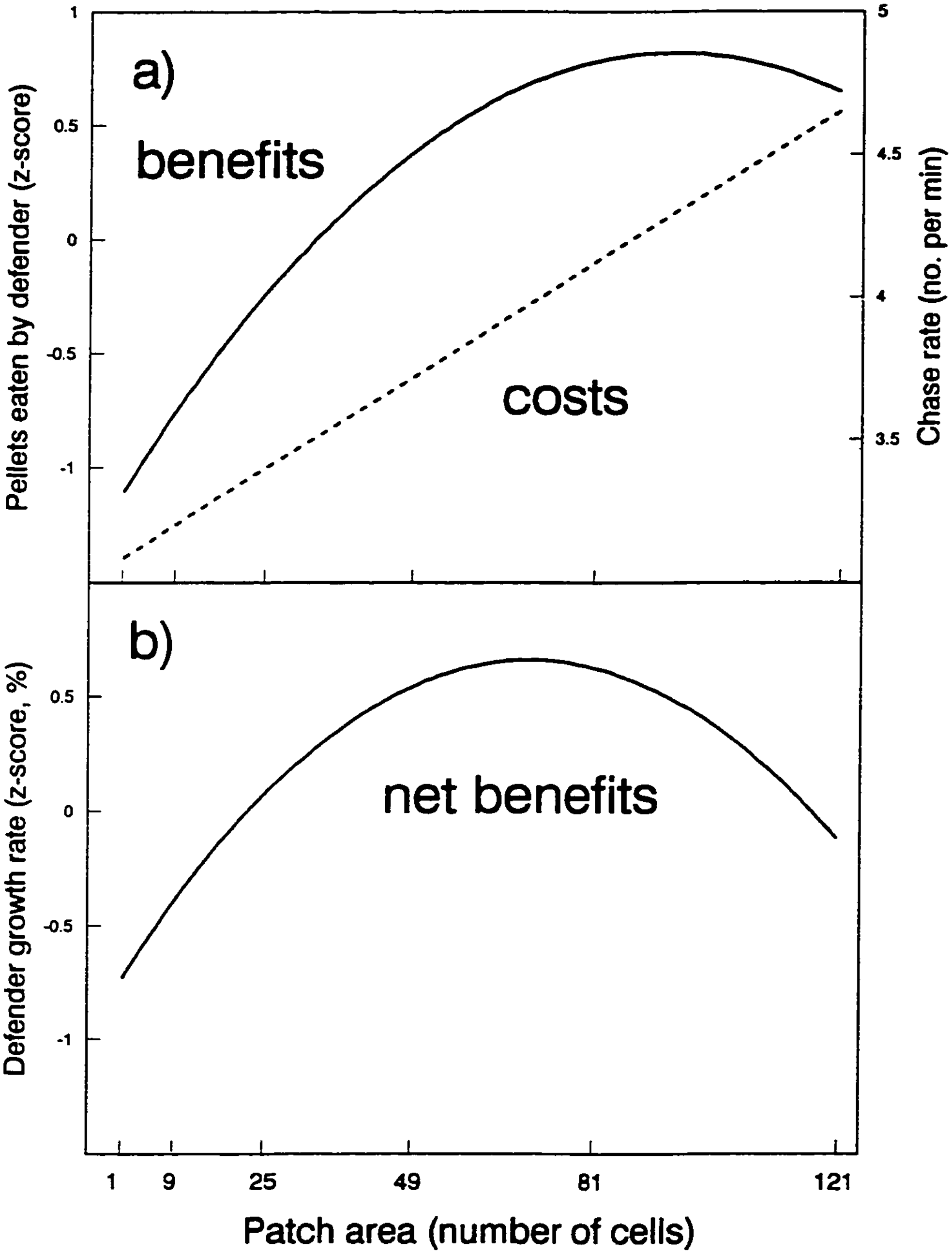

2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
Defender growth rate (residuals)
-1.5
-1
-0.5
0
0.5
1
1.5
2
Number of intruders (residuals)

Figure 17. An overview of how my study provides support for the assumptions and predictions of the simple optimal territory size model. As assumed, the benefits of defence (pellets eaten by the defender) increase in a decelerating way, whereas the costs of defence (chase rate) increase linearly with increasing territory size. As predicted, the net benefits of defence (growth rate) initially increased and then decreased as territory size increased.


a)
benefits
costs
Pellets eaten by defender (z-score)
1
0.5
0
-0.5
-1
Chase rate (no. per min)
5
4.5
4
3.5
b)
net benefits
Defender growth rate (z-score, %)
0.5
0
-0.5
-1
1
9
25
49
81
121
Patch area (number of cells)

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