

**The effects of patch shape and group size on economic defendability and growth
depensation in juvenile convict cichlids**

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The Department of Biology

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Abstract

The effects of patch shape and group size on economic defendability and growth
depensation in juvenile convict cichlids

Jae-woo Kim

While the effect of patch area on economic defendability has attracted considerable attention, there has been little research on patch shape. In addition, few studies have investigated the effects of resource defense from the perspectives of both defenders and intruders. Hence, I manipulated food patch shape independent of patch area (square, 13.6 x 13.6 cm; rectangular, 46.5 x 4.0 cm; elongated, 93.0 x 2.0 cm) and group size (three, six, twelve fish) in a 3 X 3 factorial design. I tested the predictions that the frequency of aggression, degree of resource monopolization and size variation within groups would decrease as patch perimeter and group size increased. As predicted, with increasing patch perimeter the frequency of aggression and the degree of resource monopolization decreased, but there was no change on growth depensation (size variability). Increasing the number of fish decreased the

frequency of aggression, degree of resource monopolization, leading to less size variation within groups. My study is one of the first factorial studies to manipulate the actual perimeter of the food patch to show that increasing the patch perimeter had the same effect as increasing group size on the economic defendability of a patch. My study also demonstrated that it is important to the theory of resource defense to examine the foraging success of both the defenders and intruders.

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Introduction

Animals often compete for limited resources either by directly depleting the resources (exploitation competition) or by aggression (interference competition) (Keddy 1988). Interference competition is thought to be one of major selective forces, shaping an individual's behaviour, physiology, and life history, as well as affecting a population, and its dynamics (Begon et al. 1996). According to the concept of economic defendability (Brown 1964), individuals will only defend a territory if the benefits associated with defence are greater than the energy required to defend a territory or if the net benefits of defence are greater than the alternatives.

Brown's (1964) concept of economic defendability has stimulated considerable research on two important questions: whether or not animals defend a territory, and how big a territory to defend. Of the two questions, the latter has attracted considerable research, typically framed as questions about optimal territory size. Optimality models (Dill 1978; Hixon 1980; Schoener 1983) predict that an optimal territory size occurs where the net benefit of defence (benefit – cost) is maximized. These models predict that the optimal territory size will decrease as the food abundance or intruder pressure increases. Many experimental studies (Praw & Grant 1999; Breau & Grant 2002; for a review, see Adams 2001) have now confirmed these predictions in a wide variety of taxa.

Despite considerable research on optimal territory size, there has been little work on optimal territory shape. The optimal shape of a territory is thought to be a circle, because a circle has the smallest perimeter for a given surface area (Dill 1978; Hixon 1980). Defence costs are assumed to be directly proportional to perimeter,

because intruders enter the territory across the perimeter, whereas resource abundance (i.e. benefit) is directly proportional to the area. Typically, experimenters use either a round or square patch of food in tests of resource defence theory (Monaghan & Metcalfe 1985; Theimer 1987; Prawn & Grant 1999; Goldberg et al. 2001; Grant et al. 2002).

Relatively few models (Covich 1976; Getty 1981) and only a few empirical studies (Eason 1992; Eason & Stamps 1992; Eason & Stamps 2001) have examined the effects of territory shape. Red-capped cardinals (*Paroaria gularis*) prefer a territory along the two opposite sides of a river compared to a long territory along one side of a riverbank (Eason 1992). The probability of detecting an intruder on the same shore decreased with increasing distance from the territory owner. Moreover, intruders on the opposite shore were more likely to be detected immediately than were intruders on the same shore. The reduction in defence costs due to increased intruder detectability played an important role in determining the preference of territory shape by red-capped cardinals (Eason 1992). I am not aware of any experimental studies on patch shape.

Resource defence theory also applies to the short-term defence of patches (Bryant & Grant 1995; Kim et al. 2004), and many tests of whether animals defend territories are based on such examples. The intensity of competitive aggression usually increases as resources become more clumped in space (Magnuson 1962; Monaghan & Metcalfe 1985; Ryer & Olla 1995; Grant & Guha 1993; but see Theimer 1986; Ryer & Olla 1996), dispersed in time (Grant & Kramer 1992; Grant et al. 1995; Bryant & Grant 1995; Robb & Grant 1998), predictable in space (Grand & Grant 1994), predictable in time (Goldberg et al. 2001), when of moderate abundance

(Magnuson 1962; Wyman & Hotelling 1988; Ruzzante & Doyle 1993; Grant et al. 2002), and when defended against an intermediate number of competitors (Kawanabe 1969; Warner & Hoffman 1980; Jones 1983; Magurran & Seghers 1991; Syarifuddin & Kramer 1996; Caballero & Castro-Hdez 2003).

Resource defence theory (Grant 1993) predicts a dome-shaped relationship between the frequency or intensity of aggression and group size. In small groups, interactions with conspecifics over resources are rare so the benefits of defence are low. As group size increases, the costs of defence increase but the benefits of defence increase even faster until a lower threshold is reached where the benefits exceed the costs of defence. When group size is extremely large, defence becomes uneconomical because of the high costs of excluding so many intruders. This dome-shaped prediction has been supported by only a few studies (Grant et al. 2000; Goldberg et al. 2001). In contrast, Sirot's (2002) hawk-dove game theory model predicts that aggression will increase monotonically with increasing group size, which has been observed in the bird literature (e.g. Johnson et al. 2004). However, Dubois et al. (2003) suggest that Sirot's prediction depends heavily on the assumption of pairwise interaction between competitors in hawk-dove models. If this assumption is relaxed so that multiple intruders can simultaneously challenge potential defenders, Dubois et al. (2003), and Dubois & Giraldeau's (2005) game theory models predict that aggression peaks at intermediate group size, consistent with resource defence theory (Grant 1997). Empirical studies with Japanese medaka (Grant et al. 2000) and convict cichlids (Noel et al. in press) showed that aggression peaked when the ratio of competitors to food patches (i.e. CRR, competitor-to-resource ratio, sensu Grant et al. 2000) equaled two.

Increases in the frequency or intensity of aggression typically lead to an increase in the monopolization of resources by the dominant individual in both birds (Theimer 1987; Johnson et al. 2004), and mammals (Monaghan & Metcalfe 1985). In animals with indeterminate growth, like fishes, monopolization leads to increased body size variation within groups (Kim et al. 2004). This size variation typically increases over time, a phenomenon called growth depensation in the fish literature (i.e. growth rate variability; Magnuson 1962; Ryer & Olla 1995).

Resource defence theory (Grant 1997) typically makes predictions about only one component of resource distribution at a time and assumes no interactions between components (but see Emlen & Oring 1977). However, factorial studies allow a more complete understanding than single-factor studies, because of the likely correlations of these variables in the wild (Adams 2001). A few experimental studies have investigated interactions between two components to better understand the dynamic nature of territoriality, particularly in the wild: spatial clumping and temporal clumping (Robb & Grant 1998); spatial clumping and temporal predictability (Goldberg et al. 2001); and patch size and predation risk (Kim et al. 2004). Further testing of interactions between the effects of different components of resource distribution are needed.

Traditionally, the theory of resource defence has focused on the cost and benefits of defence from the perspective of the defender. Conversely, the importance of the intruder's behaviour in the theory of territoriality has been generally ignored, with the exception of a few experimental studies (Marzluff & Heinrich 1991; Chapman & Kramer 1996; Dearborn 1998; Busch et al. 2004; Dubois & Giraldeau 2005). Chapman & Kramer (1996) examined the effect of intruder numbers on the

tactics and success of both the defender and the intruder. They found that the foraging success of intruders first increased then decreased with increasing group size.

Similarly, with increasing group size, immature common ravens (*Corvus corax*) fed at higher rates because of a reduction in neophobia and reduced aggression by territorial adults (Marzluff & Heinrich 1991). The question of how intruders behave to maximize their benefits, whether sneaking for food (Chapman & Kramer 1996), courting unguarded females (Grant et al. 1995), synchronizing intrusions with others (Foster 1985), or recruiting other intruders (Marzluff & Heinrich 1991) needs to be addressed for a richer understanding of the dynamics of interference competition.

The purpose of my study is to investigate the effects of patch shape and group size on the economic defendability of a food patch and how this affects the foraging success of both defenders and intruders. I test the predictions that (1) patches will become less defensible as patch perimeter increases, leading to lower aggression, less resource monopolization, and reduced growth depensation, (2) patches will become less defensible as group size increases, leading to lower aggression, less resource monopolization and reduced growth depensation, and (3) the foraging success of intruders will increase as patches become less defensible via increasing patch perimeter and group size. I also test (4) for interactions between the effects of patch shape and group size on aggression, resource monopolization, and growth rate variability within groups.

Materials and Methods

Experimental subjects and apparatus

I chose convict cichlids (*Archocentrus nigrofasciatus*) for my study because they exhibit considerable behavioural plasticity and readily defend patches of food in laboratory conditions (Grant & Guha 1993). Juvenile convict cichlids were used to minimize courtship behaviour and any potential behavioural differences between the sexes. Prior to the study, cichlids were held in 110 L aquaria, filled with continuously filtered, dechlorinated tap water (27°C, pH 7.2, 12:12 light:dark cycle) and were fed ad libitum, twice daily, with commercial flake food. In order to facilitate establishment of a dominance hierarchy and to recognize dominant individuals, each test tank consisted of one large fish (mean \pm SD weight = 0.37 ± 0.07 g), one medium sized fish (weight = 0.28 ± 0.05 g), and a group of small fish (weight = 0.20 ± 0.05 g). In all trials, the large fish was always the dominant individual (Keeley & Grant 1993).

Test tanks (92 x 47 x 38 cm; 164 L) contained a fully submerged heater, undergravel filter, light-coloured gravel to 3 cm in depth, and aged tap water. The back and the sides of the tanks were covered with white paper to facilitate videotaping and minimize social interactions between adjacent tanks. Lighting, temperature and pH were identical to the rearing tanks.

To test for the possible influence of patch shape and group size on competitive aggression, monopolization, and size variation, I manipulated both food patch shape and group sizes in a three-by-three factorial design. Three different shapes of patch of identical surface area (186 cm²) were made of opaque Plexiglas: square (13.6 x 13.6 cm), rectangular (46.5 x 4.0 cm), and elongated (93.0 x 2.0 cm) (Fig. 1). Group sizes of three, six, and twelve fish were used. Seven replicates of each treatment were

conducted, for a total of 63 trials, and 441 fish. Given the number of individuals needed, I used six full sibling groups and placed all fish into test tanks randomly, such that the six kin groups were equally distributed across all treatments, minimizing potential kin-biased growth (Brown & Brown 1996).

Experimental protocol

Each trial consisted of two phases: conditioning and testing. The conditioning phase lasted three days to allow fish to acclimate to test tanks and learn to feed from the patches. In order to minimize growth during the conditioning phase, 25% of the normal ration of food was given twice a day (at 9:00 and at 14:00). The testing phase lasted seven days. At 9:00 each day, fish were fed a normal ration of 0.034, 0.058, and 0.106g for each group size (3, 6, and 12). The daily ration was increased by 50 % after one week to promote growth. I spread the food pellets (Fry Feed Kiowa, approximately 1.0 mm in diameter) evenly on the gel-coated patch. The gelatin solution (7.25g / 60ml) was made of one Knox Gelatine – The Original package (7.354g) in 60 ml of hot water and applied evenly to cover the patch.

At the beginning and end of each trial, the standard length (to the nearest 0.5 mm) and weight (0.01g) of each individual were recorded. I videotaped each tank on day 5, 8, and 11 for thirty minutes, immediately following the introduction of the food patch. From the videotape, I recorded foraging and aggressive behaviour until all food was consumed, typically within five to thirty minutes of the introduction of the food patch. I also recorded the total foraging time (i.e. time until all the food was eaten) for each trial. If a trial lasted more than 30 minutes, total foraging time was considered to be 30 minutes (i.e. foraging in 14 of 189 trials lasted more than 30 minutes).

To quantify monopolization, the number of fish that were foraging within one body length of the patch was counted and its dominance status was noted (i.e. dominant versus subordinate) at one-minute intervals following the introduction of the food patch; the degree of monopolization is inversely related to the number of subordinate fish foraging. To quantify aggressive interactions, I recorded the frequency of chasing, defined as the pursuit of one fish by another for at least one body length. Aggressive interactions were recorded only if they originated within one body length of the foraging patch. I also calculated the rate of aggressive interactions per forager by dividing the total rate of aggressive interactions by the mean number of foragers in a trial, and by the total foraging time.

To quantify intruder success, I recorded the first ten intrusions per trial, defined as an intruder approaching the food patch to within one body length. For each intrusion, I counted whether the intrusion was successful, meaning that the intruder foraged in the patch (i.e. the intruder assumed the typical head-down foraging posture (see Foam et al. in press) and/or lunged towards the food patch). I also scored whether the intruder was chased by the dominant individual or left the food patch voluntarily, and noted how long each intruder stayed within the food patch. If the intruder stayed more than 60 seconds, the duration of intrusion was considered to be 60 seconds (i.e. 234 of 1884 intrusions lasted more than 60 seconds). For each trial, I calculated the average of each variable for the first ten intrusions.

Statistical analysis

I analyzed the data using repeated measures two-way ANOVAs (3 patch shapes X 3 group sizes X 3 times) and by two-way ANOVAs (3 patch shapes X 3

group sizes using the mean of the 3 times as the dependent variable). Because the repeated-measures ANOVAs were more complex and yet yielded exactly the same story as the simple two-way ANOVAs, I report the results of only the two-way ANOVAs in this thesis. To meet the assumptions required for parametric analyses, the proportion of both the dominant and subordinates foraging, the proportion of aggression by the dominant, the proportion of intruders chased, and the proportion of intruders that successfully foraged in the patch were arcsine-square-root transformed.

For all of the statistical analyses, there was only one significant interaction between the effects of patch shape and group size. Therefore, I did not report interactions unless an interaction was significant or appeared to be significant in a figure and hence required an explanation.

Results

Resource monopolization

To quantify the degree of resource monopolization, I used the indirect method of calculating the average proportion of subordinates foraging near the patch during the scan samples. As predicted, the proportion of subordinates in the patch increased with increasing patch perimeter (ANOVA: $F_{2,54} = 36.20$, $P < 0.001$; Fig. 2a). Again, consistent with my prediction, the proportion of subordinates in the patch also increased with increasing group size (ANOVA: $F_{2,54} = 33.78$, $P < 0.001$; Fig. 2a). The proportion of time that dominants were in the patch also increased with increasing patch perimeter (ANOVA: $F_{2,54} = 3.48$, $P = 0.038$; Fig. 2b). Moreover, the

proportion of time that dominants were in the patch also increased with increasing group size (ANOVA: $F_{2, 54} = 9.64$, $P < 0.001$; Fig. 2b).

Aggression

Patch shape had no significant effect on the per capita rate of aggression (ANOVA: $F_{2, 54} = 0.75$, $P = 0.48$). However, there was a significant effect of group size on per capita rate of aggression (ANOVA: $F_{2, 54} = 5.06$, $P = 0.01$); per capita rate of aggression was highest in groups of six (Fig. 3a).

Because the per capita rate of aggression does not differentiate between the number of fishes present in the tank versus the number of fishes actually foraging, I also calculated the rate of aggression per forager. As predicted, the rate of aggression per forager decreased with increasing patch perimeter (Fig. 3b; ANOVA: $F_{2, 54} = 9.05$, $P < 0.001$). Although this decrease appeared to be stronger in groups of three and six fish than in groups of twelve fish, there was no significant interaction between the effects of patch perimeter and group size (ANOVA: $F_{4, 54} = 1.62$, $P = 0.18$). The rate of aggression per forager also differed between group sizes (ANOVA: $F_{2, 54} = 10.51$, $P < 0.001$). The rate of aggression per forager was highest for groups of six, followed by groups of three, and was lowest for group size twelve (Fig. 3b).

Because several fish in a group were occasionally aggressive, I also calculated the proportion of aggression that was performed by the dominant individual. As the patch becomes less defensible and monopolizable by the dominant fish, other fish are expected to increase their level of aggression. Consistent with this prediction, the proportion of aggression by the dominant decreased with increasing patch perimeter (ANOVA: $F_{2, 54} = 12.21$, $P < 0.001$). This decrease in the proportion

of aggression by the dominant seemed stronger in groups of six and twelve than in groups of three (Fig. 4); indeed, there was a significant interaction between the effects of patch shape and group sizes on proportion of aggression by the dominant (ANOVA: $F_{4,54} = 2.71$, $P = 0.039$). As predicted, the proportion of aggression by the dominant individual also decreased as group size increased (ANOVA: $F_{2,54} = 59.30$, $P < 0.001$).

Intruder success

To examine the effect of the treatments from the intruder's point of view, I calculated the proportion of intruders that were chased by the dominant. Contrary to my expectation, there was no significant effect of patch shape on the proportion of intruders that were chased (ANOVA: $F_{2,54} = 0.41$, $P = 0.67$; Fig. 5). However, the proportion of intruders chased decreased with increasing group size (ANOVA: $F_{2,54} = 42.26$, $P < 0.001$; Fig. 5).

To investigate the effect of aggression on intruder success, I calculated the proportion of intrusions that were successful, defined as an intruder being able to forage in the patch. As predicted, the proportion of successful intrusions increased with increasing group size (ANOVA: $F_{2,54} = 33.52$, $P < 0.001$; Fig. 6a). However, patch shape had no significant effect on the proportion of successful intrusions (ANOVA: $F_{2,54} = 1.12$, $P = 0.34$). However, the average duration which intruders were allowed to remain in the patch increased with increasing patch perimeter (ANOVA: $F_{2,54} = 9.4$, $P < 0.001$; Fig. 6b). The effect of patch perimeter on intruder duration appeared to be stronger in groups of three and six than in groups of twelve, but the interaction between patch perimeter and group size was not significant

(ANOVA: $F_{4,54} = 1.55$, $P = 0.20$). The average duration of intrusions also increased with increasing group size (ANOVA: $F_{2,54} = 33.25$, $P < 0.001$; Fig 6b).

Growth rate

Contrary to my prediction, dominant growth rate did not differ between group sizes (ANOVA: $F_{2,54} = 2.01$, $P = 0.14$; Fig. 7a) or between patch shapes (ANOVA: $F_{2,54} = 1.96$, $P = 0.15$). In contrast, the growth rate of subordinates differed among group sizes (ANOVA: $F_{2,54} = 8.25$, $P = 0.001$; Fig. 7b); as expected, subordinate growth rate was lower in groups of three than in groups of six and twelve. However, there was also no significant effect of patch shape on the growth rate of subordinates (ANOVA: $F_{2,54} = 0.10$, $P = 0.90$).

To quantify growth depensation, I calculated the initial and final coefficient of variation of body mass within groups. CV final was higher than CV initial in 58 of 63 groups and was positively related to final CV (ANCOVA: effect of initial CV as a covariate: $F_{1,57} = 66.01$, $P < 0.001$). With initial CV of body mass as a covariate, the final CV of body mass differed between different group sizes (ANCOVA: $F_{2,57} = 6.68$, $P = 0.002$); final CV of body mass for groups of three was higher than the groups of six and twelve (Fig. 8). However, final CV of body mass did not differ significantly among different patch shapes (ANCOVA: $F_{2,57} = 1.01$, $P = 0.37$).

Discussion

Patch shape

Increasing patch perimeter had a significant effect on only four of 10 variables (Table 1). However, all four significant responses were in the predicted direction. As patch perimeter increased, the proportion of subordinates foraging in the patch increased as well as the duration of each subordinate foraging attempt, whereas the rate of aggression per forager and the proportion of aggression by the dominant individual decreased.

Curiously, these significant behavioural changes did not translate into a decrease in the dominant's growth rate or the variability of body size within groups (i.e. growth depensation) (Robb & Grant 1998). Presumably, any gains in monopolization by the dominant individual in the square patch were offset by an increased amount of energy devoted to defence (Breau & Grant 2002). The dominant fish in the square patch appeared to chase each intruder a longer distance than those occupying less defensible patches (i.e. rectangular or elongated) (personal observation). Hence, the dominant spent less time in the square patch or rectangular patch than the elongated patch. This increased cost of aggression (Praw & Grant 1999; Breau & Grant 2002) may have led to a lower net benefit. The ability of the dominant to see the whole patch may have prompted it to defend the whole patch, whether economically feasible or not (see Praw & Grant 1999). Hence, square patches may have been indivisible (Praw & Grant 1999), whereas the elongated patch was more likely to be defended by several fish. Alternatively, the dominant fish may have suffered a greater level of physiological stress defending the square patch than

subordinate fish (Koebele 1985) leading to a more uniform size variability within groups for each treatment.

Group size

Not surprisingly, increasing group size had a significant effect on 9 of 10 variables (Table 1). Seven of the 9 effects were as predicted. As predicted, increasing group size resulted in an increase in intruder foraging success and growth rate, which led to lower CV of body size within groups (Syarifuddin & Kramer 1996; Savino & Kostich 2000).

Per capita chase rate and chase rate per forager showed a dome-shaped relationship with increasing group size. As predicted by resource defence theory (Grant 1997) and a modified hawk-dove model (Dubois et al. 2003; Dubois & Giraldeau 2005), aggression was highest at the intermediate group size of six, followed by groups of three, and then lowest at groups of twelve (Fig. 9a, b; Caballero & Castro-Hdez 2003). However, this peak in aggression at a CRR of 6 was higher than previously reported in fishes (Grant et al. 2000; Noel et al. in press). The chase rates were low for group size three, because it was easy for the dominant to defend against two intruders in any shape of patch (Fig. 4). Alternatively, it may be more difficult to apply the theory of CRR (i.e. competitor-to-resource ratio; Grant et al. 2000) to this study due to the indivisible nature of the food patch in some treatments, but not in others. In previous studies (Grant et al. 2000; Noel et al. in press), resources were clearly divisible items: mates, food items, or ice cube trays containing food. As predicted, the proportion of aggression by the dominant also decreased with increasing group size (Fig. 9c). The cost of defending the patch by the dominant

increased with increasing group size, leading to a higher participation level by others in aggression. The decrease in both the aggression and resource monopolization led to a decrease in variability of growth rate and/or decrease in growth depensation as in other studies (Blanckenhorn 1992; Smith & Fuiman 2003).

Interestingly, the growth rate of the dominant did not differ between different group sizes. Although the dominant fish in groups of three monopolized the food patch to a greater extent, the dominant may have eaten less food, because of the lower total amount of food available. Curiously, the dominant spent more time in the patch with increasing group size perhaps because it had switched from interference competition to scramble competition.

Intruder success

Contrary to my expectations, increasing patch perimeter had relatively little effect on the foraging success of intruders. Patch perimeter had a significant effect on only two (i.e. proportion and duration of subordinates foraging) of four measures of intruder success (Table 1).

In contrast, increasing group size had the predicted positive effect on all four measures of intruder foraging success. The proportion of successful intrusions increased with increasing group size causing an increase in the benefit of intrusion (Dubois et al. 2004). This is consistent with higher foraging level attained by the subordinates as group size increased. Moreover, the proportion of intruders chased decreased with increasing group size leading to a reduction in the cost of intrusions. This allows intruders to forage more freely and/or suffer less injury or physiological stress associated with aggressive interactions. Again, as predicted the average

duration of intrusions also increased with increasing group size (Chapman & Kramer 1996), leading to a higher benefits for intruders. The longer the intruder is allowed to forage in the patch, the more likely it is to feel like the owner of the patch (Smith 1978; Arcese 1987). This may explain why some intruders begin defending when the patch can no longer be defended and monopolized by the dominant, leading to a reduced growth depensation.

General implications

My experiment is not meant to represent the actual foraging competition of convict cichlids in the wild. However, convict cichlids are an excellent model system for testing resource defence theory, because selection in the wild should strongly favour faster growth. Faster growing individuals mature earlier and/or at a greater size, larger males monopolize breeding sites (Wisenden 1995) and mate with larger females (Keenleyside 1985), and larger females are more fecund (Nuttall & Keenleyside 1993) and outcompete smaller females for access to males with breeding sites (Wisenden 1995). Hence, juveniles compete intensely for food even in my artificial laboratory experiment.

In aquaculture and/or laboratory conditions where aggression is higher than in natural conditions (Cleveland 1999), it is important to avoid unnecessary aggression and to reduce growth depensation within groups. My study provides a practical method of reducing aggression and monopolization via increasing patch perimeter, and decreasing aggression, and growth depensation via increasing group size.

Table 1. Predicted and observed effects of patch perimeter and group size on different variables.

Variable	Increasing patch perimeter		Increasing group size	
	Predicted ¹	Observed	Predicted	Observed
Proportion of subordinates in patch	↑	↑	↑	↑
Per capita chase rate	↓	—	↓	∧
Chase rate per forager	↓	↓	↓	∧
Prop. of aggression by dominant	↓	↓	↓	↓
Prop. of intruders chased	↓	—	↓	↓
Prop. of successful intrusions	↑	—	↑	↑
Duration of intrusion	↑	↑	↑	↑
Dominant growth rate	↓	—	↓	—
Subordinate growth rate	↑	—	↑	↑
CV final	↓	—	↓	↓

¹↑ Variable increased with increasing patch perimeter or group size

↓ Variable decreased with increasing patch perimeter or group size

— Not significant; i.e. $P > 0.05$

∧ Dome-shaped relationship between the variable and increasing patch perimeter or group size

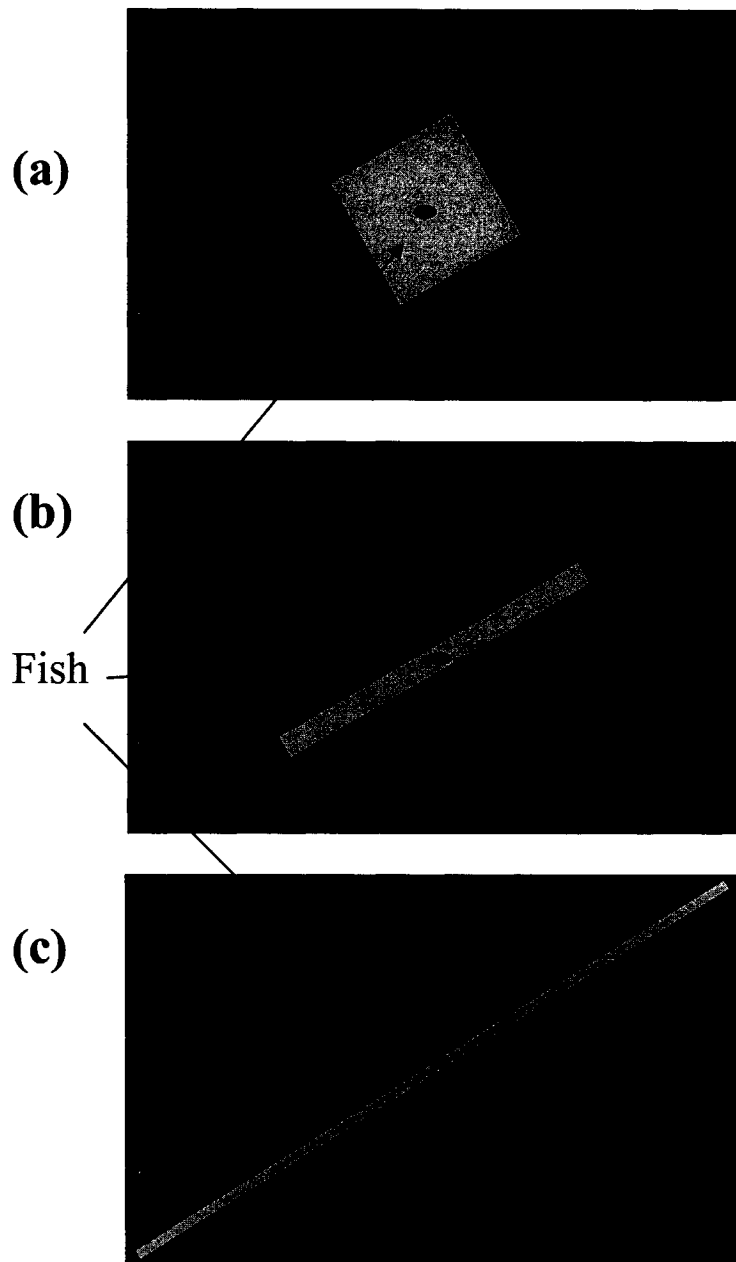


Figure 1. Diagrams of top view of the tanks illustrating the three shapes of food patch, all 186 cm^2 in area but differing in perimeter: (a) square, 54.4 cm; (b) rectangular, 101.0 cm; (c) elongated, 190.0 cm. The black oval in the middle of each patch illustrates the relative size of the average fish (mean \pm SD: Length = $1.85 \pm 0.21 \text{ cm}$) in relation to food patch, and the tank.

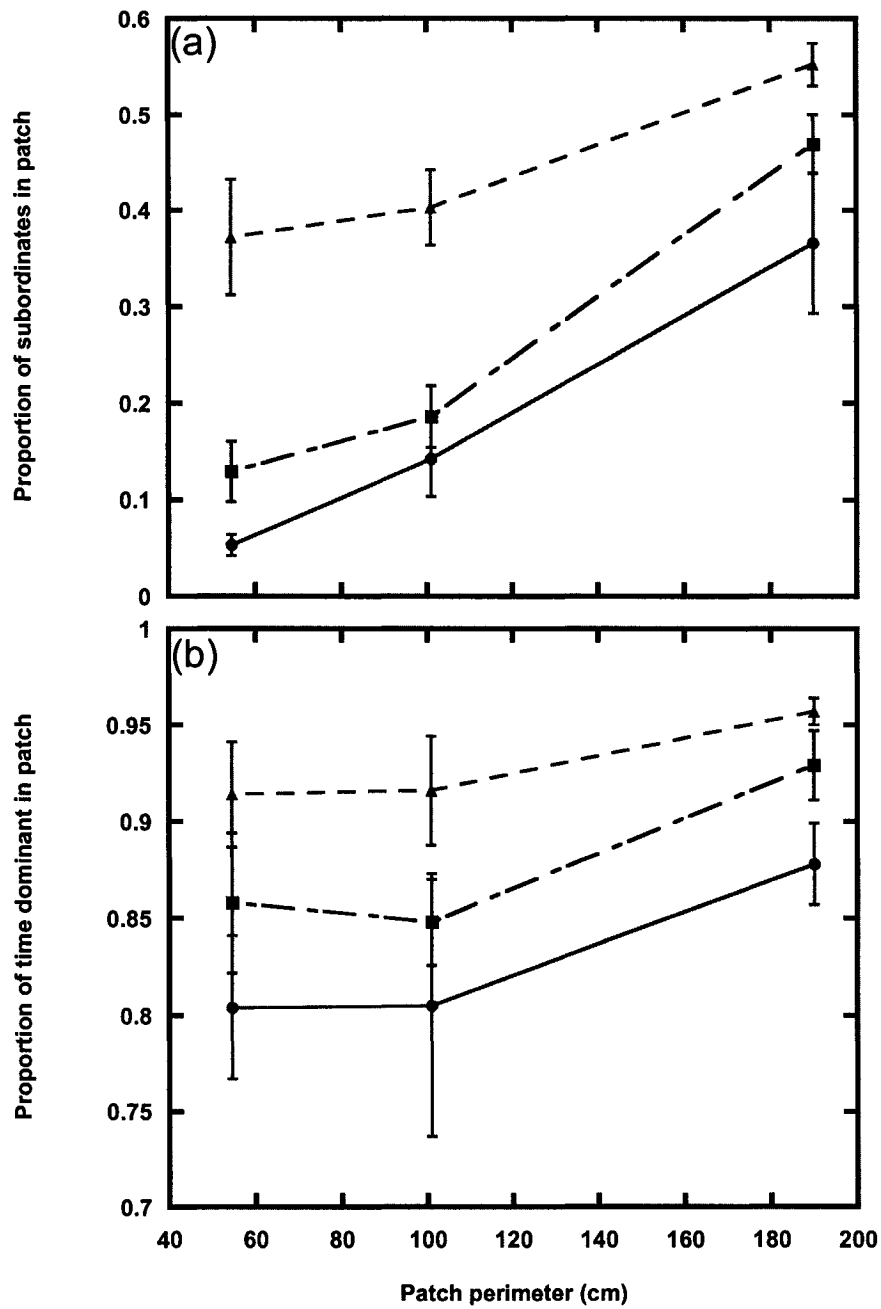


Figure 2. Mean (\pm SE, $N = 7$) (a) proportion of subordinates within one body length of the patch, and (b) proportion of time the dominant was in the patch, for groups of three (●), six (■), and twelve (▲) in relation to patch perimeter.

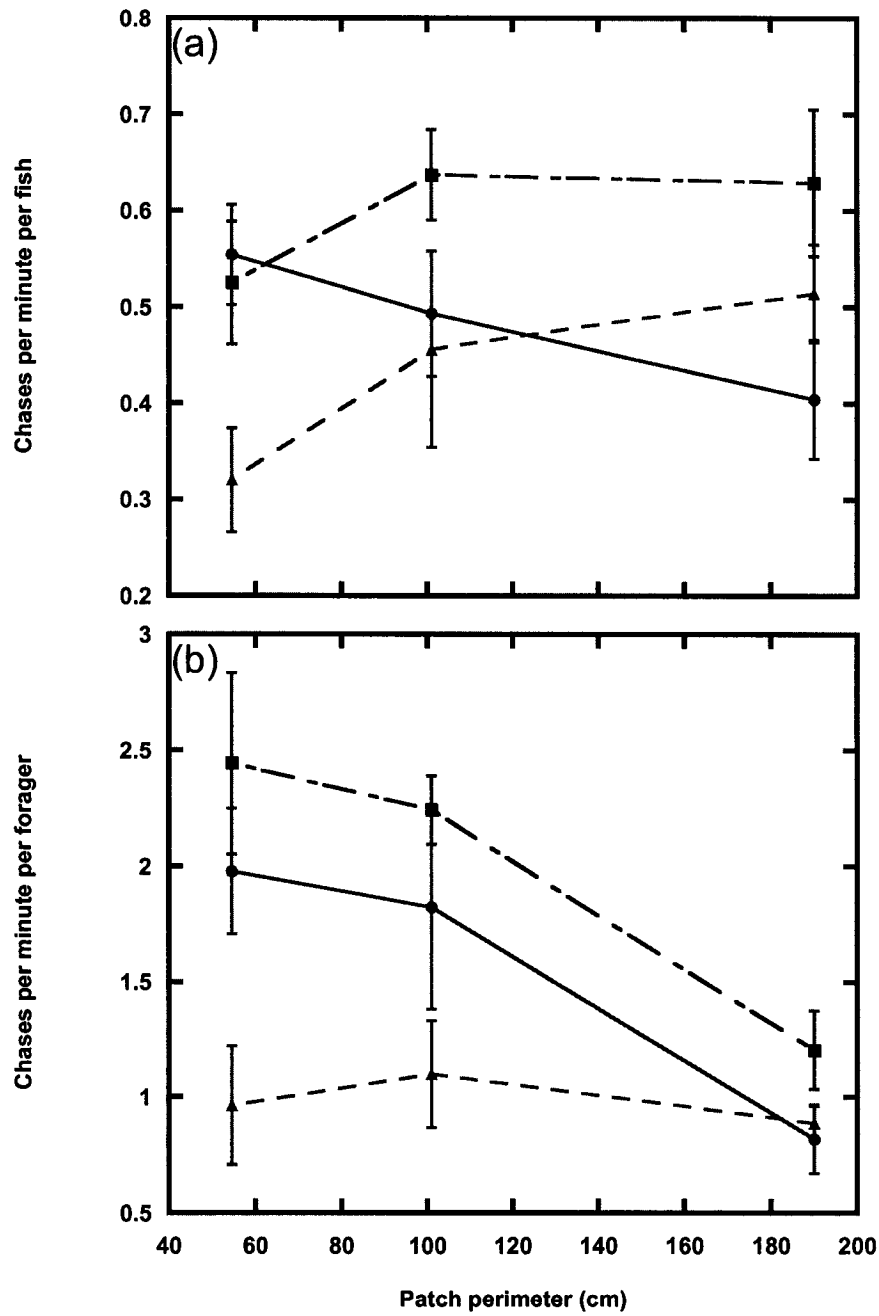


Figure 3. Mean (\pm SE, $N = 7$) (a) per capita rate of aggression, and (b) rate of aggression per foraging fish, for groups of three (●), six (■), and twelve (▲) in relation to patch perimeter.

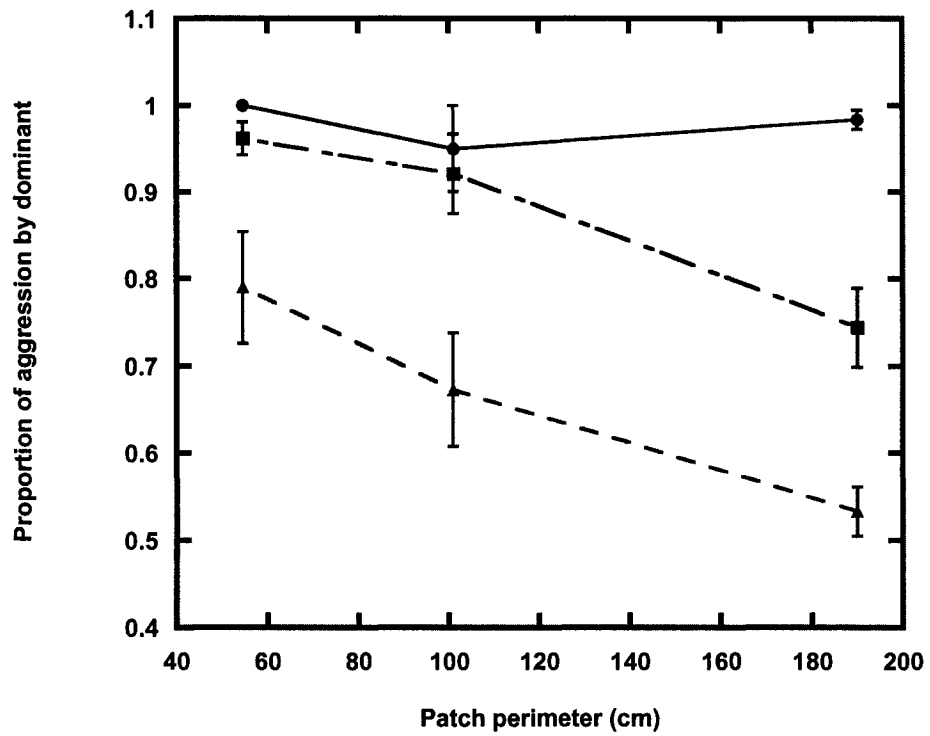


Figure 4. Mean (\pm SE, $N = 7$) proportion of aggression by the dominant fish for groups of three (●), six (■), and twelve (▲) in relation to patch perimeter.

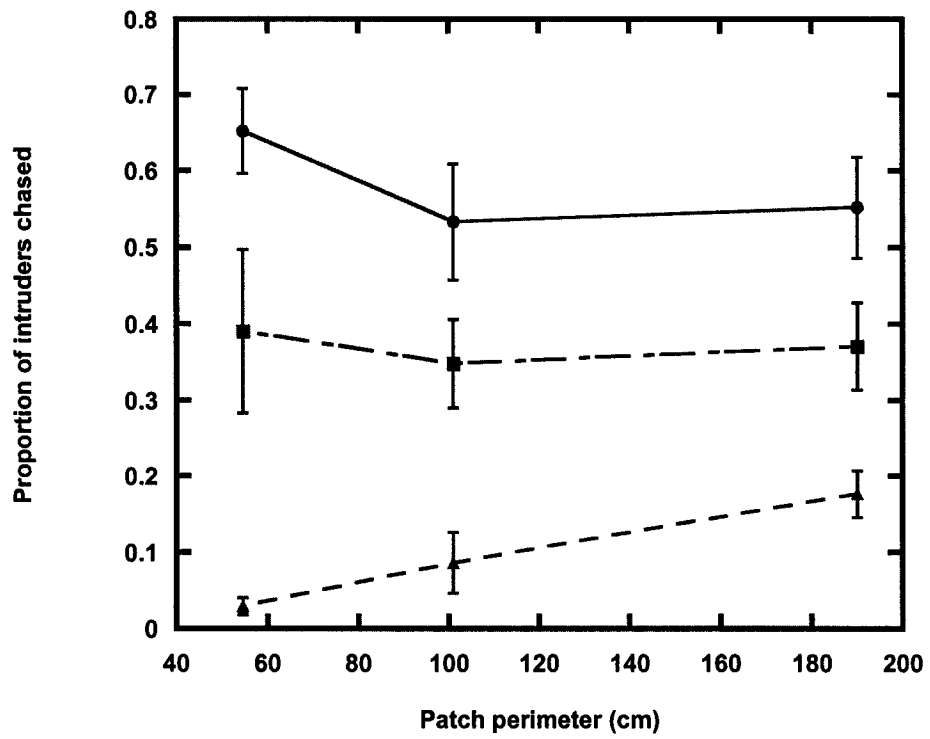


Figure 5. Mean (\pm SE, $N = 7$) proportion of intruders chased for groups of three (●), six (■), and twelve (▲) in relation to patch perimeter.

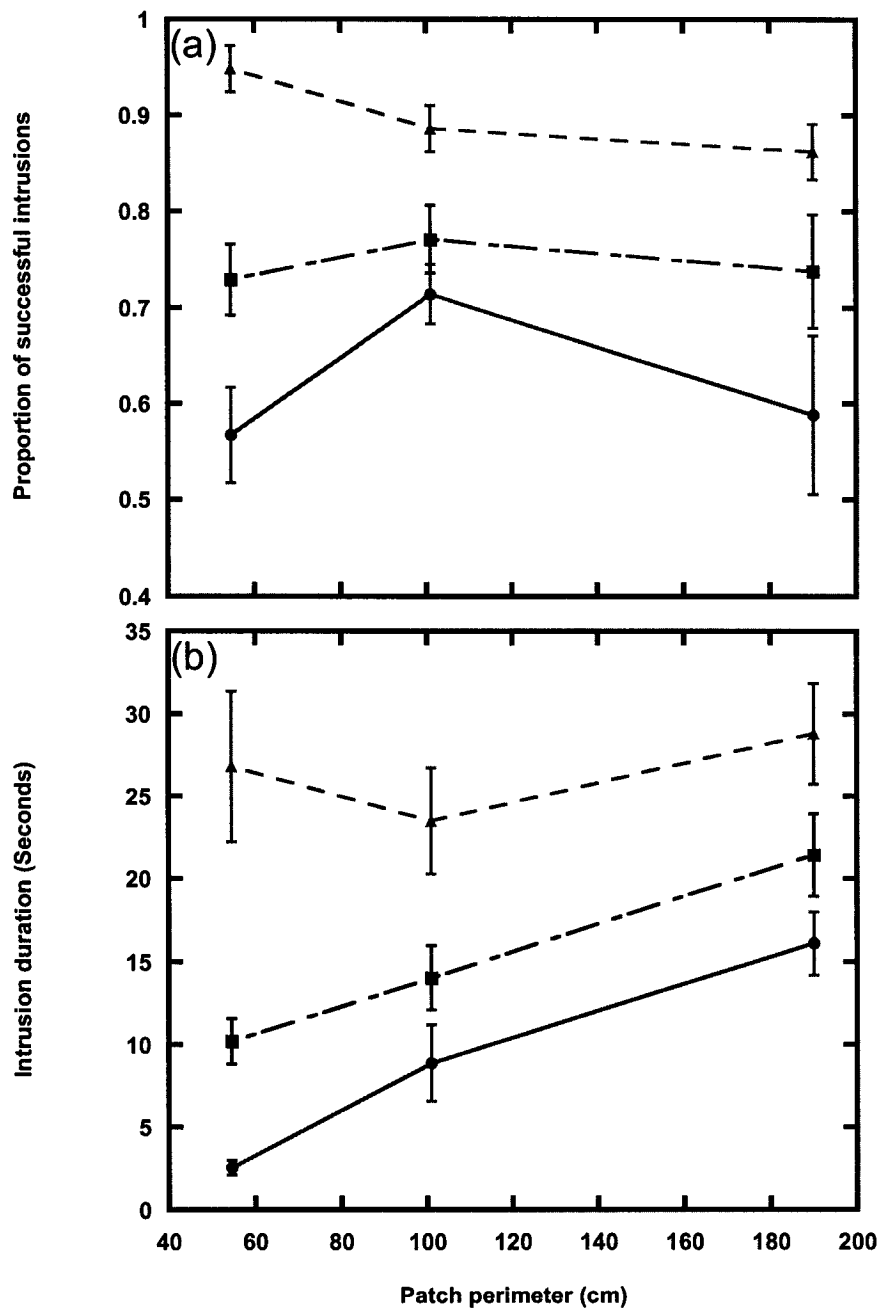


Figure 6. Mean (\pm SE, $N = 7$) (a) proportion of intruders that successfully foraged in the patch, and (b) average duration of intrusion, for groups of three (●), six (■), and twelve (▲) in relation to patch perimeter.

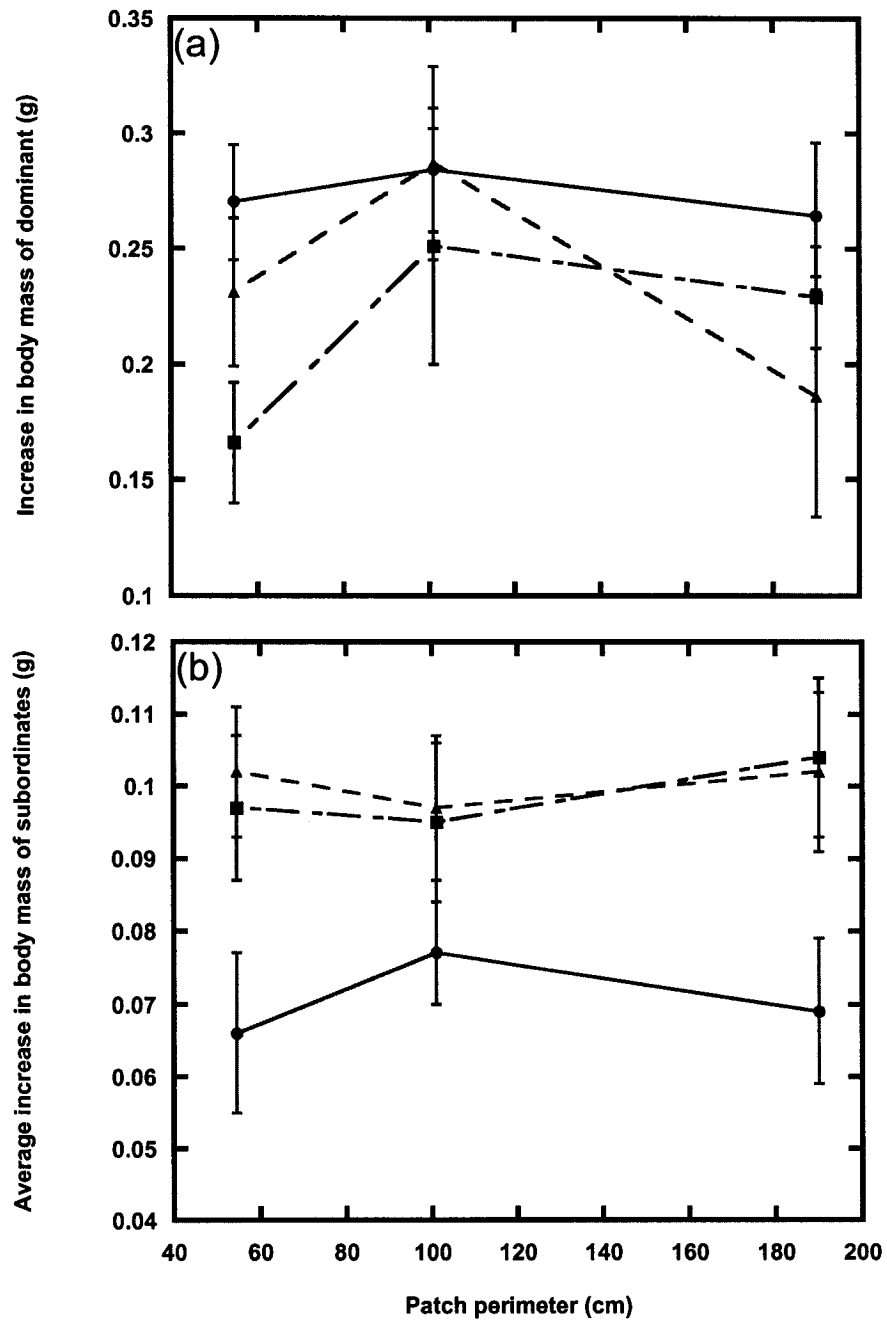


Figure 7. Mean (\pm SE, $N = 7$) (a) dominant growth rate, and (b) average growth rate of subordinates, for groups of three (●), six (■), and twelve (▲) in relation to patch perimeter.

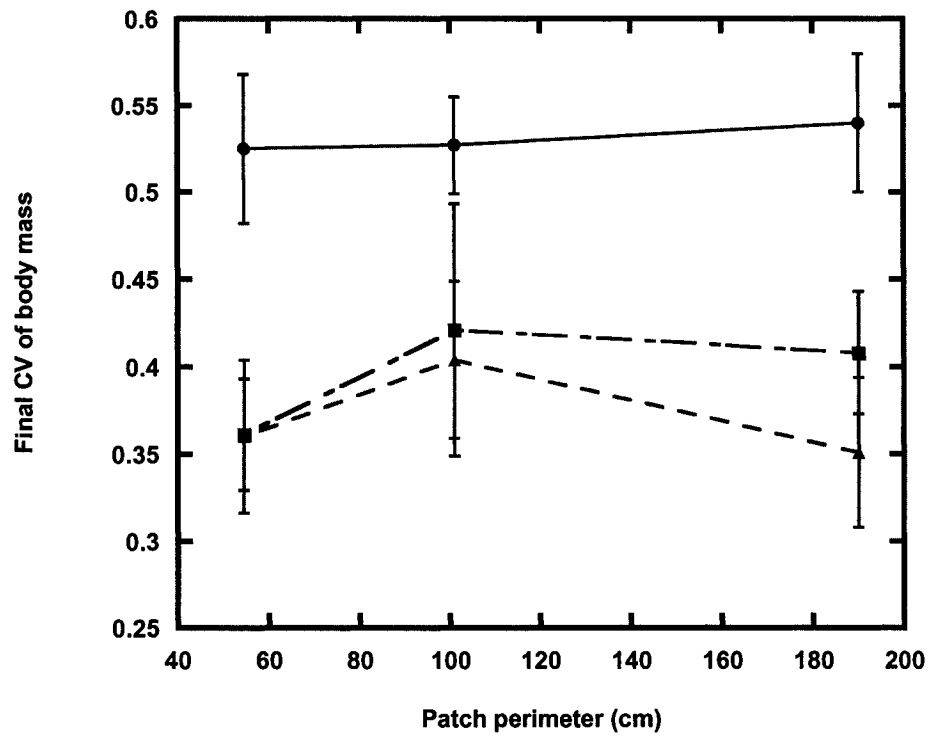


Figure 8. Mean (\pm SE, $N = 7$) final CV of body mass for groups of three (●), six (■), and twelve (▲) in relation to patch perimeter.

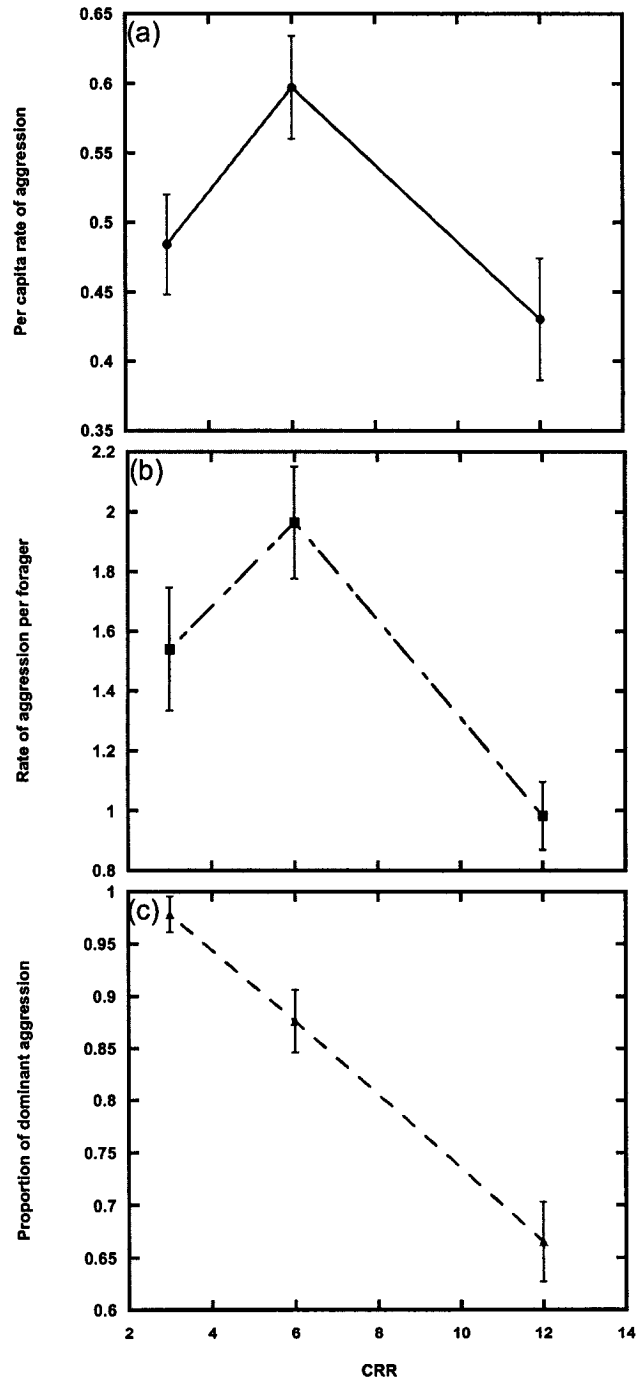


Figure 9. Mean (\pm SE, $N = 7$) (a) per capita chase rate (\bullet), (b) chase rate per forager (\blacksquare), and (c) proportion of aggression by the dominant (\blacktriangle), in relation to CRR (competitor-to-resource ratio) of 3, 6, and 12.

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