Effect of food abundance on aggressiveness and territory size of juvenile rainbow trout, *Oncorhynchus mykiss*

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How food abundance affects (1) whether or not individuals defend territories and (2) what size of territory is defended, are crucial to understanding the role that territoriality plays in regulating the population size of stream-dwelling salmonids. The threshold model of feeding territoriality predicts that territorial defence will be most intense at intermediate levels of food abundance, whereas optimal territory-size models predict that territory size will decrease with increasing food abundance. While the latter prediction has been supported by several studies of stream salmonids, too few levels of food abundance were typically used to describe the exact relationship between territory size and food abundance. Hence, to quantify the relationship between the intensity of defence and territory size in relation to food abundance, we manipulated food abundance over a broad range of values (0.62, 1.25, 2.5, 5, 10, and 20% of the fish wet body weight in dry food per day) in artificial stream channels (1.92 x 0.77m), while monitoring the territorial behaviour of juvenile rainbow trout, *Oncorhynchus mykiss*. As predicted by the threshold model of feeding territoriality, the frequency of territorial aggression was highest at intermediate levels of food abundance, but fish never ceased defending territories entirely, particularly at food densities likely found in the wild. Also as predicted, the aggressive radius of rainbow trout decreased significantly, but only by 30% over a 32-fold increase in food abundance, equivalent to a 51% decrease in territory size. Our results suggest that territory size was relatively insensitive to changes in food abundance, and may have a regulatory effect on population density.

Keywords: juvenile salmonids, food density, territoriality, optimal territory size, aggressive behaviour

37 The threshold model of feeding territoriality originally predicted that animals defend
38 territories between a lower and upper threshold of food abundance in an all-or-none fashion
39 (Carpenter & MacMillen 1976; Wilcox & Ruckdeschel 1982; Carpenter 1987). However, when
40 individual variation was incorporated into resource defense theory, a more continuous change in
41 aggression was predicted (Wolf 1978; Craig & Douglas 1986; Grant 1997). As food abundance
42 increases, the frequency or intensity of territorial aggression initially increases continuously from
43 low-intensity scramble competition to the infrequent defence of non-exclusive territories, to the
44 vigorous defence of exclusive territories, (Craig & Douglas 1986; Grant 1993) and then
45 decreases continuously as food becomes superabundant. Therefore, the threshold model of
46 territoriality, or its more continuous version, predict either an upper and lower threshold for
47 defence or a dome-shaped relationship between the frequency or intensity of territorial
48 aggression and food abundance, respectively (Grant 1993).
49 Considerable evidence of the variability in how frequently individuals defend territories
50 or whether or not territories are defended at all has now been documented in various taxa
51 (Wilcox & Ruckdeschel 1982; Monaghan & Metcalfe 1985; Lott 1991; Goldberg et al. 2001;
52 Grant et al. 2002(). While many studies show a decrease in aggression as food abundance
53 increases (i.e. the right side of the dome-shaped relationship: Magnuson 1962; Slaney &
54 Northcote 1974; Johnson et al. 2004), fewer studies have shown an increase in aggression as
55 food abundance initially increases (i.e. Newman 1956; Keenleyside & Yamamoto 1962), and
56 even fewer have documented the dome-shaped relationship (i.e. Wyman & Hotaling 1988; Grant
57 et al. 2002). Given that an individual defends a territory, optimality models (Hixon 1980;
58 Schoener 1983) predict that territory size will decrease with an increase in food abundance and

intruder pressure (Schoener 1983). These predictions have now been supported by many studies in a variety of taxa defending both ephemeral and more permanent territories (Grant 1997; Adams 2001).

Juvenile stream dwelling salmonids defend feeding territories against conspecifics under laboratory and field conditions (Slaney & Northcote 1974; Dill et al. 1981; Keeley 2000; Imre et al. 2004). Because territory size can limit the abundance of juvenile (Grant & Kramer 1990; Elliott 1994) and adult (Jonsson et al. 1998) salmon, any environmental factor that reduces territory size should increase their population density (Grant et al. 1998). Hence, describing the exact relationship between territory size and important environmental variables, such as food abundance, are crucial to understanding the role that territoriality plays in regulating population size. The territory size of juvenile salmonids is inversely related to food abundance in both observational field (Keeley & Grant 1995; Keeley & McPhail 1998) and experimental laboratory (Slaney & Northcote 1974; Keeley 2000; but see Imre et al. 2004) studies. However, laboratory studies typically use only three levels of food abundance, making it difficult to describe the quantitative relationship between territory size and food abundance. If fish vary the size of their territory to maintain a constant abundance of food, then territory size is predicted to be inversely proportional to food abundance (a slope of -1.0), and salmonid abundance will be regulated by food abundance rather than territorial behaviour (Grant et al. 1998). For example, a doubling of food abundance would cause a halving of territory size and a doubling of salmonid abundance. However, a review of the available data indicated that a doubling of food abundance causes territories to shrink by only 25% (Grant et al. 1998).

Our study had two primary goals. First, we tested the competing predictions of the threshold model of territoriality and the more continuous version of the model: (1) territoriality will cease entirely when food abundance is low or in excess; or (2) the frequency of territorial aggression will follow a dome-shaped relationship over a broad range of food abundance. Second, we quantified the relationship between territory size and food abundance in juvenile rainbow trout over a 32-fold increase in food abundance. Specifically, we tested these competing predictions: with increasing food abundance territory size (3) does not change; (4) decreases with a slope of -1.0; or (4) decreases with a slope that is shallower than -1.0.

MATERIALS AND METHODS

Experimental Subjects

We obtained 400 young-of-the-year (YOY) rainbow trout from Pisciculture Arpents Verts, Ste-Edwidge-de-Clifton, Québec, Canada. The trout were kept in holding tanks filled with filtered, dechlorinated water on a 12-hour light: 12-hour dark cycle. Water temperature varied throughout the experimental period from 14 to 22°C in May-July and from 14 to 18.7°C in September-November, within the preferred temperature range for rainbow trout (Kerr & Lasenby 2000). The fish were fed daily with Vigor # 4 floating feed (Corey Feed Mills) while in holding tanks. Three hundred and sixty trout were used in the experiments. After the experiments were completed, all fish were euthanized with MS-222 as per animal care protocol AREC-2010-GRAN issued to JWA Grant by the Concordia University Animal Research Ethics Committee in accordance with the guidelines of the Canadian Council on Animal Care.

Experimental Set up

Experiments were carried out in artificial stream channels (1.92 x 0.77 m) filled with continuously recirculating (approximately 10% new water per day), filtered, dechlorinated tap water to a depth of approximately 20 cm (mean ± SD = 19.7 ± 2.1 cm) on a 12 hour light: 12 hour dark cycle (09:00-21:00). Current velocity was recorded at three different points in each tank at the end of each trial (mean ± SD = 0.032 ± 0.017 m/s). Water temperature varied with the outdoor temperature and was measured daily for each trial (mean ± SD temperature = 17.23 ± 2.43 °C). The bottom of each tank was covered with a layer of aquarium gravel overlaid by a four by eight grid of cobbles (mean diameter = 7.84 cm; range = 5.7-10.5 cm). The cobbles were placed with their centres 15.3 cm apart along the width and 21.3 cm apart along the length of the tank and were used as visual markers to facilitate estimating the relative position of individuals as well as to aid fish in establishing territories (La Manna & Eason 2003). Each stream channel was stocked with 12 fish (mean ± SD fork length = 4.20 ± 0.22 cm; mean ± SD mass = 1.18 ± 0.28 g), equivalent to 8 YOY/m^2, corresponding to a high density for fish of this size in the wild (Grant & Kramer 1990). The experimental treatments consisted of six different food levels: 0.62, 1.25, 2.5, 5, 10, and 20% of the fish wet body weight in dry food per day. Each food level was a multiple of the highest amount of food typically encountered by juvenile salmonids in the wild (Keeley 2000), equivalent to 5% of the wet body weight in dry food (Imre et al. 2004). Each of the food treatments was replicated 5 times, with each trial lasting 7 days. The daily ration of food (Optimum 0.7 granulated fish feed, Corey Feed Mills) was spread evenly on an automatic belt feeder that dispensed the food at the upstream end of the channel at a constant rate over the 12-hour "daylight" period.

126 *Data Collection*

127

128 Trials were carried out from May-July and September-November 2010. Prior to each
129 trial, the initial fork length (to the nearest mm) and body weight (to the nearest 0.01g) of
130 individuals were recorded. Individuals were given a unique mark with fluorescent elastomer tags
131 in the dorsal and/or caudal fins to allow for individual identification. Fish were given a
132 conditioning period of approximately 24 hours before the beginning of each trial to allow them
133 to acclimate to the new environment and to the method of food delivery. On the final day of each
134 trial, a scan sample was conducted in order to record the position of each fish on a schematic
135 map. Then, each individual was observed independently for 15 minutes to record the distance
136 and frequency of aggressive acts, such as charges, chases, and nips (sensu Keenleyside &
137 Yamamoto 1962), and the location of each station (sensu Steingrímsson & Grant 2008) from
138 which aggressive acts were initiated. The grid of labeled cobbles acted as a simple x-y coordinate
139 system, with the 0,0 (x,y) position in the downstream left corner of stream channel. Following
140 the observation, the final fork length and weight of all individuals were recorded. Specific
141 growth rate was calculated for all individuals as $G = (\log_e W_{Final} - \log_e W_{Initial}) / t$, where G is the
142 specific growth rate of weight (*W*) increase and *t* is the duration of the trial in days (Ricker
143 1975).

144 In each tank one dominant individual defended a large portion of the stream channel. Of
145 the remaining individuals, called subordinates, some were aggressive while being subordinate to
146 the dominant fish. Aggressive subordinates included territorial individuals that defended a fixed
147 area (sensu Maher & Lott 1995) and "floaters" (sensu Puckett & Dill 1985) that did not defend
148 fixed home ranges or maintain a station, but occasionally displayed aggressive behaviour.

Territories were relatively exclusive areas, except that subordinate territorial individuals did not chase the dominant. The aggressive rate was obtained for all individuals in each tank by counting the number of aggressive acts during focal animal observations.

In each tank, the defended area of all territorial fish was estimated by calculating the individual's mean aggressive radius, the distance between the location of the chasee and the position of the chaser when the aggressive act was initiated. We did not estimate territory size using the minimum convex polygon technique because it is sensitive to sample size (i.e. frequency of aggression; Schoener 1981), which varied considerably among treatments. However, mean aggressive radius will be unbiased by differences in the frequency of aggression between trials. The number of territorial subordinates per trial varied from 2 to 11, so we calculated two territory size measurements for each trial: the average chase radius of the dominant fish and the mean of average chase radii for each territorial subordinate. At the lowest food abundance, the dominant fish did not show any aggressive behaviour over the course of observation in 2 of the trials, and were excluded from the calculation of aggressive radius. To compare our data with those from the literature, we estimated territory area by first calculating the average aggressive radius for all the fish in a trial and then assuming that territories are circular (see Keeley & Grant 1995).

Statistical Analysis

Because food levels increased in a geometric series, we $\log_{10}$-transformed the food abundance before fitting regressions. To meet the assumptions of parametric tests, aggressive radius was also $\log_{10}$-transformed. Because the dominant individual defended a relatively large

portion of the stream compared to other fish, a two-way ANOVA was used to determine whether there was a main effect of dominance status (dominant versus subordinates) and food treatment on aggressive radius and growth rate. Only significant interactions between dominance status and food treatment were reported in the results.

Average water temperature and initial fork length of individuals were added as covariates in all analyses. Initial fork length of the fish did not have a significant effect on any variable, whereas water temperature had a significant effect on aggressive radius. Thus, we reported the results of the two-way ANCOVA in the section on aggressive radius. SPSS ver. 12.0.1 was used for all statistical tests ($\alpha = 0.05$).

RESULTS

General Behaviour

At the beginning of trials, fish initially gathered at the downstream end of the streamchannel. Within 1-2 days, a dominant fish moved upstream and defended an area of the stream channel directly downstream of the feeder. Subordinate territorial individuals (2-11 per trial) defended territories immediately downstream of the dominant's defended area, whereas floaters existed in the spaces between territories of other fish. Non-aggressive fish occupied undefended home ranges at the downstream end of the stream channel. While dominant fish were initially larger than subordinates (dominants: mean ± SD mass = 1.30 ± 0.30 g; subordinates: mean ± SD mass = 1.17 ± 0.26; paired t-test: $t_{29} = 6.82$, $P < 0.001$), dominant fish were the largest in their groups in only 13 of 30 cases. At the end of the 7-day trials, dominants were still larger than subordinates (dominants: mean ± SD mass = 2.28 ± 0.60 g; subordinates: mean ± SD mass = 1.58 ± 0.67 g; paired t-test: $t_{29} = 10.37$, $P < 0.001$). and were the largest fish in 21 of 30 cases

197 *Frequency of Aggression*

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199 The total number of aggressive acts over the course of the 15-minute observation period
200 differed significantly across the food treatments (Fig. 1a; ANOVA: $F_{5, 24} = 11.10$, $P < 0.001$).
201 The total rate of aggression initially increased with increasing food abundance and then declined
202 when food was abundant, as indicated by a significant quadratic term in a polynomial regression
203 after the linear term was first entered in the model ($t_{27} = 4.51$, $P < 0.001$). On average, the fish
204 engaged in 130 aggressive acts per 15-minute observation during the 5% treatment, whereas
205 aggression rate dropped to only 45 acts per 15 minutes when food was scarce (i.e. 0.63%) or
206 abundant (i.e. 10 and 20%). Fish were satiated and did not eat all the food during the 10 and 20%
207 treatments.

208 The dome-shaped pattern of total aggression was related to two other measures of
209 aggression. The percentage of individuals engaging in aggression also differed among food
210 treatments (ANOVA: $F_{5, 24} = 4.70$, $P = 0.004$). About 40% of individuals were aggressive at low
211 and high levels of food abundance compared to 60-70% at intermediate levels of food abundance
212 (Fig. 1b). The per capita rate of aggression by the aggressive fish also differed significantly
213 among the levels of food abundance (ANOVA: $F_{5, 24} = 11.03$, $P < 0.001$). As with the other
214 measures, the per capita rate of aggression initially increased with increasing food abundance,
215 peaked at intermediate level of food abundance, and then decreased (Fig. 1c). Both relationships
216 (Figs. 1b, c) were confirmed by a significant quadratic term in a polynomial regression ($t_{27} =$
217 3.18, $P = 0.004$ and $t_{27} = 4.92$, $P < 0.001$, respectively).

218

219 *Territory Size*

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221 Water temperature had a significant positive effect on aggressive radius (two-way
222 ANCOVA: $F_{1, 43} = 10.07$, $P = 0.003$), and hence was included as a covariate in all analyses.
223 Mean aggressive radius of the focal fish differed significantly across food treatments (two-way
224 ANCOVA: $F_{5, 43} = 3.46$, $P = 0.01$) and decreased with increasing food abundance for both
225 dominant and subordinate fish (Fig. 2; two-way ANCOVA, linear contrast: $P = 0.005$). Overall,
226 dominant fish had a larger aggressive radius than subordinate fish (two-way ANCOVA: $F_{1, 43} =$
227 12.50, $P = 0.001$).

228

229 *Growth*

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231 As food abundance increased, the growth rate of all subordinates increased at a faster rate
232 than dominant individuals as indicated by a significant interaction between dominance status and
233 food treatment (Fig. 3; two- way ANOVA: $F_{5, 48} = 19.56$, $P < 0.001$). In spite of the significant
234 interaction, the specific growth rate of focal fish increased with increasing food abundance for
235 both dominant (ANOVA, linear contrast: $F_{1, 24} = 10.05$, $P = 0.004$) and subordinate individuals
236 (ANOVA, linear contrast: $F_{1, 24} = 504.20$, $P < 0.001$). Growth rate appeared to decline at the
237 highest food level, but the difference between the 10 and 20% treatments was not significant
238 (Tukey post hoc tests: dominant fish: $P = 0.966$; subordinate fish: $P = 0.422$). Dominant fish
239 grew faster than subordinate individuals in all food treatments except the 10 (Tukey post hoc
240 test: $P = 0.998$) and 20% (Tukey post hoc test: $P = 0.999$) treatments.

241

242 *Territory Size versus Food Abundance*

We compared the effect of food abundance on territory size in our study to that of Slaney & Northcote (1974) and Keeley (2000); both studies introduced young rainbow trout to three levels of food abundance (Fig. 4). Because the absolute amount of food could not be easily compared between studies, territory size and food abundance were transformed to multiples of the mean territory size and food abundance for each study. Like previous studies, territory size in our study changed inversely with food abundance (Fig. 2), confirming the prediction of models of optimal territory size (Schoener 1983). However, the relationship in our study had a shallower slope compared to those of Slaney and Northcote (1974) and Keeley (2000) (Fig. 4); the mean slopes in their studies were above the 95% C.I. about the slope in our analysis. All the observed slopes were shallower than the slope of -1.0, suggesting that territory size changed less than one would expect if fish were maintaining a constant amount of food in their territories.

DISCUSSION

As predicted by the continuous version of the threshold model of territoriality, there was a dome-shaped relationship between the frequency of aggression and food abundance, indicating that fish modified their aggressive behaviour to conspecifics in response to changes in food abundance. Despite the broad range of food abundance used, dominant rainbow trout never ceased defending territories in our experiment. As mentioned in the Introduction, many studies show a decrease in aggression when food is superabundant (i.e. Magnuson 1962; Slaney & Northcote 1974), mainly due to satiation. In natural streams, however, food abundance is variable and tends to be lower than the rations provided in laboratory experiments (see Keeley 2000). Thus, only large temporary increases in invertebrate production, such as caused by heavy

rainfall or an emergence of insects (Waters 1966), would likely cause satiation of fish in natural streams. On the other hand, in the absence of satiation, fish increase their territorial aggression when food abundance increases - i.e. the left side of the dome-shaped relationship (Keenleyside & Yamamoto 1962; Newman 1956). Hence, our study suggests that the intensity of territoriality (e.g. percent of intruders chased) will increase monotonically over the range of food densities typically found in the wild. However, we cannot rule out the possibility that the increase in aggression rate was due to an increase in the rate of intrusion on territories (see Grant & Guha 1993). The only other studies to document a dome-shaped relationship between aggression and food abundance also used a broad range of food abundance with aggression decreasing when food was in excess (Wyman and Hotaling 1989; Grant et al. 2002).

As predicted by models of optimal territory size (Hixon 1980; Schoener 1983), the aggressive radius of dominant fish decreased with increasing food abundance. However, a doubling of food abundance caused territories to shrink by only 13% of their initial size, which is much less than the 50% decrease in defended area that would be expected if fish varied the size of their territories to maintain a constant supply of food (Grant et al. 1998). Both Slaney and Northcote (1974) and Keeley (2000) reported a steeper decrease in territory size with increasing food abundance. The steeper slopes in their studies may have been related to fish being allowed to emigrate, which resulted in a decrease in fish density when food abundance was low. Thus, changes in territory size in their studies were caused by changes in both intruder pressure and food abundance. By contrast, in our study fish density was held constant and changes in territory size were the result of changes in food abundance alone.

Stream fertilization has been considered as a habitat management option to increase salmonid abundance in nutrient deficient streams (Slaney et al. 1994). The 32-fold increase in food abundance in our experiment caused territories to shrink to only 51% of their initial size, suggesting that an increase in food abundance would have a relatively small effect on territory size and fish population density in mesotrophic streams (Grant et al. 1998). However, the 32-fold increase in food abundance caused the growth rate of individual fish to increase by 9 fold, suggesting that an increase in food abundance may increase salmonid abundance primarily by affecting the individual growth rate rather than the population density. Similar to our results, a review of four stream fertilization experiments (Grant et al. 1998) revealed that most of the increase in salmonid abundance resulted from an increase in growth rate rather than an increase in population density. Increased growth rate can be beneficial to fish populations, because it can increase the overwinter survival of juveniles (e.g. Hunt 1969) and decrease the age of fish migrating to sea (Hutchings & Jones 1998). However, an increased growth rate can also cause a higher proportion of sexually mature male parr (Hutchings & Jones 1998), which may reduce the number of anadromous males returning to spawn. Hence, any attempt to enhance salmonid populations by increasing the productivity of the stream should carefully consider the potential benefits and costs of increasing the growth rate of individuals.

As expected, dominant individuals occupied a central upstream foraging station, and had a priority of access to food items as they fell from the feeder. While dominant fish were not initially always the largest individual, they had a larger aggressive radius and a higher growth rate than subordinates over the course of the experiment. Consistent with our results, the dominant status of juvenile Atlantic salmon is influenced more by an individual's aggression

than its size (Huntingford et al. 1990; Thorpe et al. 1992). Dominant fish often have a higher growth rate than subordinates (Yamagishi 1962; Li & Brocksen 1977), mainly due to differential access to food (Yamagishi 1962). In addition, the social stress caused by dominant fish may result in a higher metabolic rate and lower growth rate of subordinates (Millidine et al. 2009), even if the food consumption by dominant and subordinates is equal (Abbott & Dill 1989; Lee et al. 2011).

Laboratory studies may overestimate the fitness advantage of dominant individuals in the wild (Höjesjö et al. 2002). Natural environments are more complex than simple laboratory environments and may weaken the strength of social interactions. For example, structural complexity can reduce territory size (Imre et al. 2002), lower aggression, reduce the monopolization of food (Basquill & Grant 1998; Sundbaum & Naslund 1998) and decrease the growth advantage of dominant individuals (Höjesjö et al. 2004). In complex habitats, aggressive fish may not be able to monopolize food as efficiently, due to a decrease in their ability to detect (Savino & Stein 1982) and chase intruders (Stamps 1984). Therefore, the differences between dominants and subordinates observed in our experiment may be less extreme in a natural stream.

In summary, in our experiment the frequency of territorial defence increased and territory size decreased over the range of food abundance expected to be found in the wild. Because territory size was relatively insensitive to changes in food abundance, territoriality should have a regulatory effect on population density.

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471 Figure Captions

Figure 1. Effect of food abundance on mean (± SE, N = 5) (a) number of aggressive acts ($Y = -117.36 \log_{10}X^2 + 126.57 \log_{10}X + 69.37$, $r^2 = 0.43$, $P < 0.001$), (b) proportion of aggressive individuals ($Y = -40.96 \log_{10}X^2 + 39.52 \log_{10}X + 55$, $r^2 = 0.29$, $P = 0.009$), and (c) per capita aggressive rate of aggressive fish (chases/fish/min) ($Y = -0.71\log_{10}X^2 + 0.74 \log_{10}X + 0.41$, $r^2 = 0.48$, $P < 0.001$). The solid lines represent the quadratic regressions. Note the logarithmic scale on the x-axis.

Figure 2. Mean (± SE, N = 5) aggressive radius of dominant (●) and aggressive subordinate fish (■) in relation to food abundance. The lines represent linear regressions (solid line: $\log_{10}Y = -0.10 \log_{10}X + 1.55$, $r^2 = 0.19$; dotted line: $\log_{10}Y = -0.11 \log_{10}X + 1.46$, $r^2 = 0.26$). Note that N = 3 for dominant fish in the 0.63% treatment and the logarithmic scale on both the axes.

Figure 3. Effect of food abundance on mean (± SE, N = 5) specific growth rate of dominant (●) and the average subordinate fish (■) in relation to food abundance. Note the logarithmic scale on the x-axis.

Figure 4. Effect of food abundance (multiples of the mean) on territory size (multiples of the mean). The solid line is the predicted territory size if fish defend a constant amount of food. Note the logarithmic scale on both axes.

Figure 1

494

495

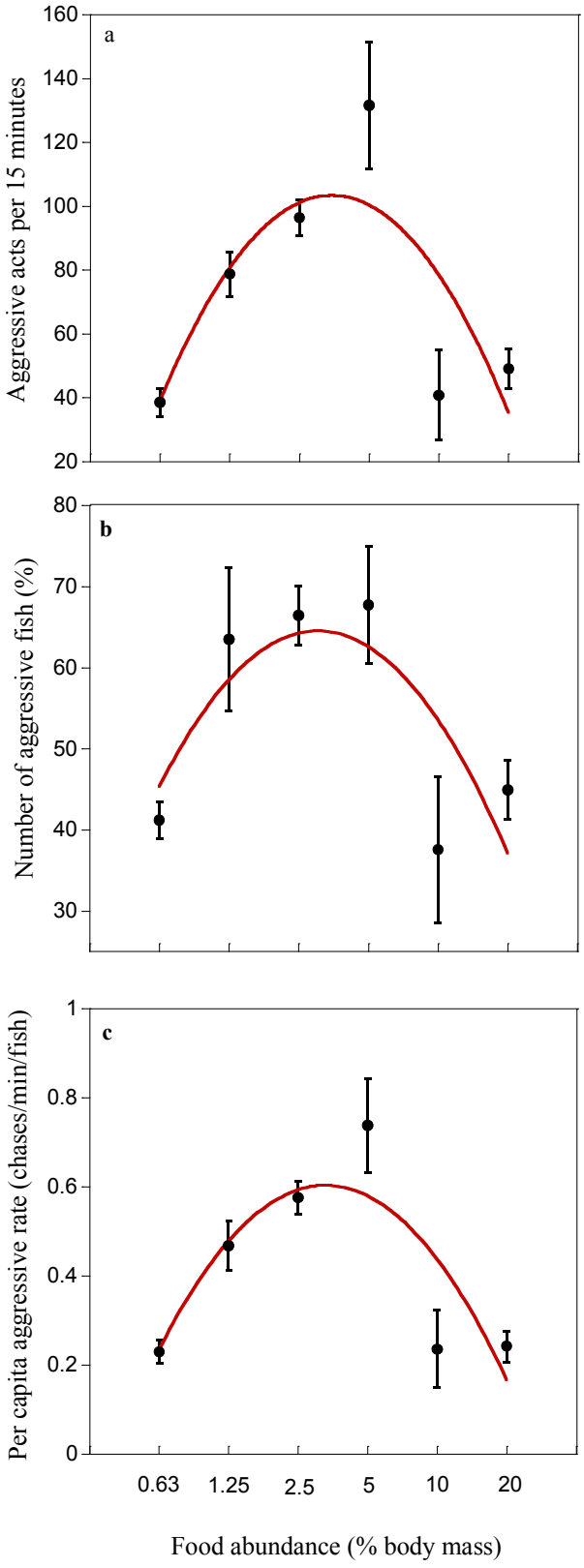

a
Aggressive acts per 15 minutes
160
140
120
100
80
60
40
20
b
Number of aggressive fish (%)
80
70
60
50
40
30
c
Per capita aggressive rate (chases/min/fish)
1
0.8
0.6
0.4
0.2
0
0.63
1.25
2.5
5
10
20
Food abundance (% body mass)

Figure 2

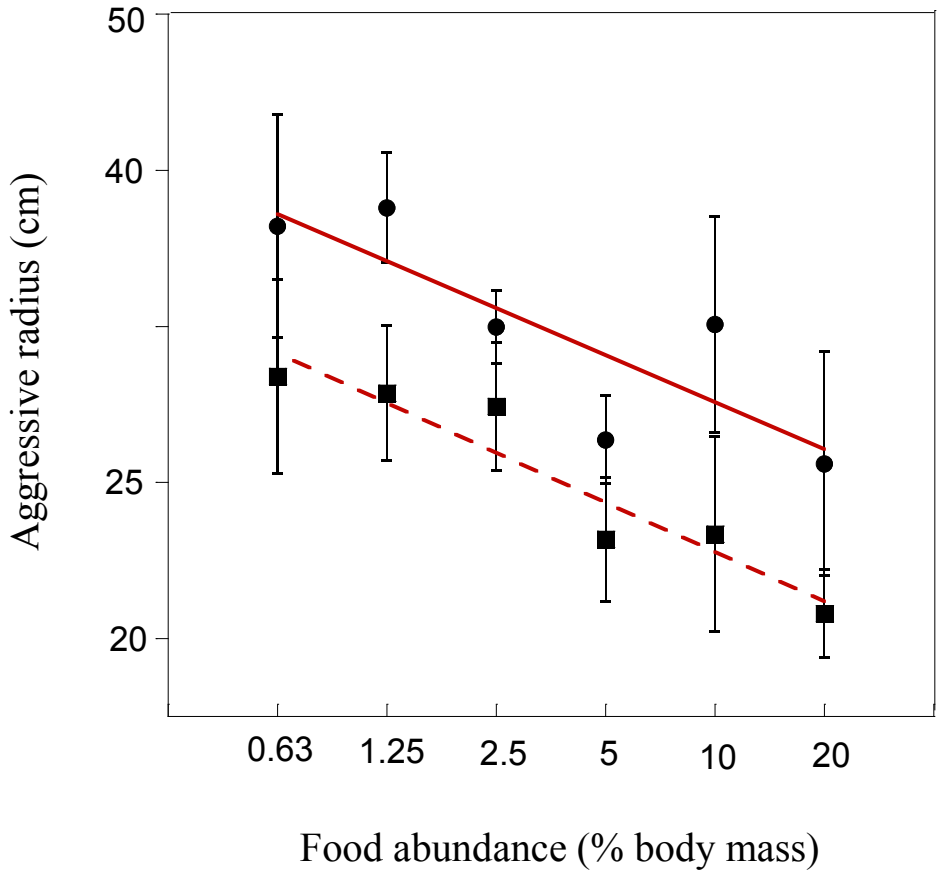

Aggressive radius (cm)
50
40
25
20
0.63
1.25
2.5
5
10
20
Food abundance (% body mass)

Figure 3

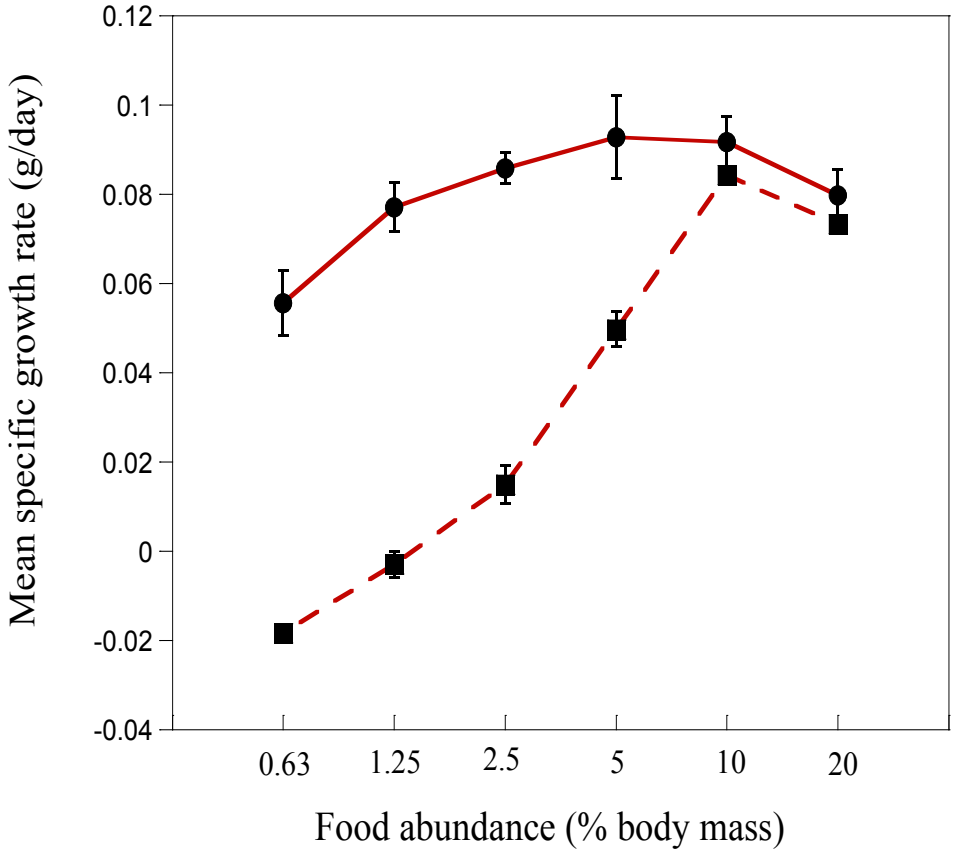
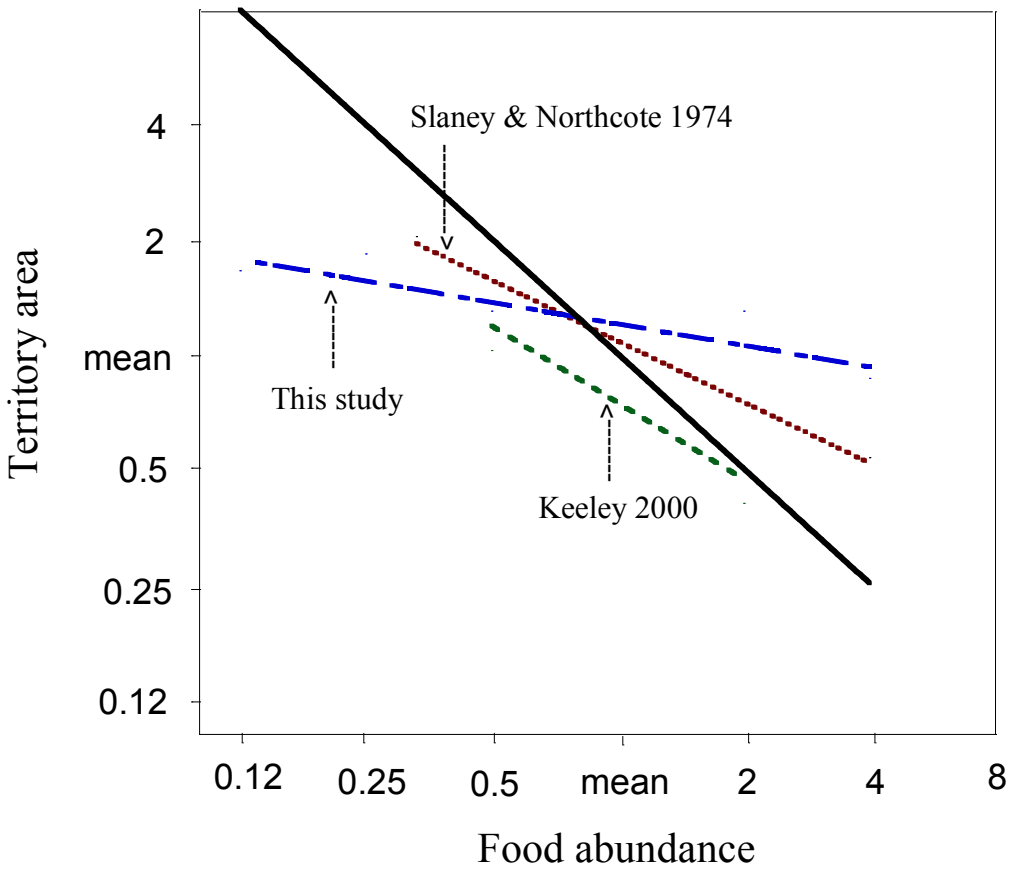

Mean specific growth rate (g/day)
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
0.63
1.25
2.5
5
10
20
Food abundance (% body mass)

Figure 4


Slaney & Northcote 1974
This study
Keeley 2000
Territory area
4
2
mean
0.5
0.25
0.12
0.12
0.25
0.5
mean
2
4
8
Food abundance