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

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Abstract

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Territoriality is thought to be an important mechanism of population regulation in stream-dwelling salmonids. Since territory size can limit salmonid abundance, describing the exact relationship between territory size and important environmental variables, such as food abundance, is crucial to understanding the role that territoriality plays in regulating population size. The threshold model of feeding territoriality predicts that: (1) territories will occur between a lower and upper threshold of food abundance, and (2) the frequency of territorial aggression peaks at intermediate levels of food abundance. Optimal territory size models predict that territory size should decrease with an increase in food abundance. While this prediction has now been supported by a limited number of studies in salmonids too few levels of food abundance were used to describe the quantitative relationship between territory size and food abundance. Hence, I 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 per day) in artificial stream channels (1.92 x 0.77m) and monitored the territorial behaviour of juvenile rainbow trout (*Oncorhynchus mykiss*). First, I tested the prediction of the threshold model of territoriality: a dome-shaped relationship between territorial aggression and food abundance. Second, I quantified the relationship between territory size and food abundance over a 32-fold increase in food abundance by testing the following predictions: with increasing food abundance, territory size (1) does not change; (2) decreases with a slope of -1.0; or (3) decreases with a slope that is shallower than -1.0. Consistent with the prediction of the threshold model of feeding territoriality, the number of aggressive individuals peaked at the intermediate levels of food abundance. For the fish that were aggressive, there was a dome-shaped relationship between the frequency of territorial aggression and food abundance. As predicted by the models of optimal territory size, the aggressive radius of rainbow trout decreased with increasing food abundance but with a shallower slope than – 1.0, suggesting that territory size changed less than one would expect if fish were maintaining a constant amount food in their territory. The results of my study suggest that an increase in food abundance would have a relatively small effect on territory size and thus on the density of juvenile salmonids.

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Introduction

Animals often compete for limiting resources, such as food, shelter or mates, by defending territories and excluding others from specific areas (Brown 1964; Grant 1997). According to the theory of economic defendability, animals should only defend territories if the fitness benefits of defense exceed the costs (Brown 1964), or if the net benefits of defense exceed the net benefits of alternative tactics. The decision of whether or not to defend is influenced by a variety of factors including competitor density, resource density, and resource distribution in space and time (Brown 1964). An ideal economically defendable resource is moderately dense, spatially clumped, temporally dispersed, and spatially and temporally predictable (Grant 1997).

The threshold model of feeding territoriality predicts that animals defend feeding territories between a lower and upper threshold of food abundance (Carpenter and MacMillen 1976; Carpenter 1987). Below the lower threshold, food is too scarce and does not pay the costs of defense, so that territorial individuals will have a lower fitness compared to non-territorial ones. Above the upper threshold, when food is superabundant, non-territorial individuals gain the same amount of food as territorial ones without paying the cost of defense (Grant et al. 2002). Hence, territoriality is beneficial only between the lower and upper thresholds of food abundance (Wilcox and Ruckdeschel 1982; Davies and Houston 1984).

According to early versions of the threshold model of territoriality, animals were predicted to defend or not defend a territory in an all-or-non fashion, with changes in behaviour occurring at the threshold switch points (Carpenter and MacMillen 1976). However, resource defense theory combined with variation among individuals predicted a more continuous change in aggression as food abundance increased (Wolf 1978; Craig and Douglas 1986). As food abundance increases, the frequency or intensity of territorial aggression initially increases continuously from infrequent, low-intensity scramble competition to frequent, escalated fighting (Dubois et al. 2003) and then decreases as food becomes superabundant. Therefore, the threshold model of territoriality predicts a dome-shaped relationship between the frequency or intensity of territorial aggression and food abundance (Grant 1993).

In contrast to this dome-shaped prediction, the hawk-dove model (Parker 1984) predicts that territorial aggression decreases with increased food abundance (Sirot 2000). The reason for the contrasting predictions of the two models might be due to the assumptions of the hawk-dove model (Grant et al. 2002). First, in the hawk-dove model, interactions occur only when individuals compete for food items. However, in predictable environments animals defend empty patches in anticipation of food arrival (Grant and Kramer 1992). Interaction in the absence of food decreases the fitness of the hawk and thus decreases the probability of playing hawk in the population (Sirot 2000). Second, interactions are only between two competitors. However, when food is scarce many individuals compete and aggregate at the best food patches, making aggression uneconomical (Dubois et al. 2003). When these assumptions are relaxed, the hawk-dove model is expected to make similar predictions to those of resource defense theory (Dubois et al. 2003).

Considerable evidence of behavioural plasticity in territorial behaviour has now been documented in various taxa, such as birds (Goldberg et al. 2001), fish (Grant et al. 2002), and mammals (Monaghan and Metcalfe 1985). While many studies show a decrease in aggression as food abundance increases (i.e. the right side of the dome-shaped relationship; Magnuson 1962; Slaney and Northcote 1974; Johnson et al. 2004), fewer have shown an increase in aggression as food abundance increases (i.e. Keenleyside and Yamamoto 1962; Newman 1965), and even fewer have documented the dome-shaped relationship (i.e. Wyman and Hotaling 1988; Grant et al. 2002).

Given that an individual decides to defend a territory, an important question is how large an area should be defended. Optimality models (Hixon 1980; 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 various taxa (Ebersole 1980; Frazblau and Collins 1980; Eberhard and Ewald 1994). However, optimal territory size models assume that animals defend non-contiguous territories. That is, unoccupied space between neighbouring territories allows individuals to expand their defended areas without constraints from neighbouring territories (Grant 1997). However, such models may not be appropriate when animals defend contiguous territories in which territory holders are not free to expand their territories. Contiguous territories are often smaller than the non-contiguous optimum due to the territorial pressure from their contiguous neighbours (Hixon 1980; Grant 1997). Only Hixon (1980) has considered contiguous territories in his model, which predicts that territory size will decrease with increasing intruder pressure and increasing food abundance, but only if food abundance is sufficiently high (Keeley 2000). Two experimental field studies investigated the independent effects of food and competitor abundance on the size of contiguous territories in reef fishes and found that an increase in intruder pressure decreased territory size

(Tricas 1989), whereas food abundance had little (Tricas 1989), or no effect on territory size (Norman and Jones 1984).

Juvenile stream dwelling salmonids have been a popular model system for studies of territoriality. Juvenile salmonids defend feeding territories against conspecifics under laboratory and field conditions (Slaney and Northcote 1974; Dill et al. 1981; Keeley 2000; Imre et al. 2004) and occupy contiguous territories at high population densities (Keenleyside 1979). Territorial behaviour is an important potential mechanism of population regulation in salmonids (Grant and Kramer 1990; Elliott 1994). Because territory size can limit salmonid abundance, 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. In the field, territory size of juvenile salmonids has been shown to be inversely related to food abundance (Keeley and Grant 1995; Keeley and McPhail 1998). However, only a few studies have measured territory size while manipulating food abundance in the laboratory. For example, Keeley (2000) and Slaney and Northcote (1974) introduced young rainbow trout (*Oncorhynchus mykiss*) to different food levels and found that territory size decreased significantly with increasing food abundance. However, both studies used 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 is predicted to be directly proportional to food abundance (a slope of 1.0)

(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 limited literature data indicated that a doubling of food abundance causes territories to shrink to only 75% of their initial size (Grant et al. 1998). Imre et al. (2004) attempted to quantify the relationship between food abundance and territory size by presenting six levels of food densities to juvenile rainbow trout in artificial stream channels. They found that food abundance had no significant effect on territory size, perhaps because fish were very young and most did not actively defend territories. Moreover, the density of fish in their experiment was very high (24.8 fish/m^2), which might have made it difficult for territory holders to expand territories when food abundance was low (see Hixon 1980).

My study had two primary goals. First, I tested the prediction of the threshold model of territoriality: the frequency of territorial aggression should follow a dome-shaped relationship over a broad range of food abundance. Second, I quantified the relationship between territory size and food abundance in juvenile rainbow trout over a 32-fold increase in food abundance. Specifically, I tested the following predictions: with increasing food abundance territory size (1) does not change; (2) decreases with a slope of -1.0; or (3) decreases with a slope that is shallower than -1.0.

Materials and Methods

Experimental subjects

The fish used in my experiment were young-of-the-year (YOY) rainbow trout purchased from Pisciculture Arpents Verts, Ste-Edwidge-de-Clifton, Quebec, 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 18.7 to 14°C in September-November. This range was within the preferred temperature range for rainbow trout (Kerr and Lasenby 2000). The fish were fed daily with Vigor # 4 floating feed (Corey Feed Mills) while in holding tanks.

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 (diameter = 7.84 cm; range = 5.7-10.5 cm). The cobbles were placed 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 and 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, which is the highest density typically found in the wild for fish of this size (Grant and Kramer 1990; Wood 2008). 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 is 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. Since stream-dwelling salmonids feed primarily on drifting invertebrates (McNicol et al. 1985; Keeley and Grant 1995), food was presented in a manner simulating natural stream drift. 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.

Data collection

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

In each tank one dominant individual typically defended a large portion of the stream channel. Of the remaining individuals, called subordinates, some were aggressive while being subordinate to the dominant fish. Aggressive subordinates included fish that defended territories and "floaters" (sensu Puckett and Dill 1985) that did not defend fixed home ranges or maintain a station but occasionally displayed aggressive behaviour. 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 the dominant and aggressive subordinates 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. In the analysis of aggressive radius, I included dominants with at least 2 chases and any aggressive subordinates with at least one chase over the course of the 15-minute observation. The number of subordinates chasing per trial varied from 2 to 11. So, I used the average chase radius of aggressive subordinates in each trial. At the lowest food abundance, the dominant fish did not show any aggressive behaviour over the course of observation in 2 of the trials. Therefore, they were excluded from the calculation of aggressive radius.

Statistical analysis

One-way ANOVAs were performed to determine whether frequency of aggression, number of aggressive individuals, and the specific growth rate differed across food treatments. Polynomial regressions were also used to test for the linear or quadratic changes in the frequency of aggression and number of aggressive individuals in relation to changes in food abundance. Because food levels increased in a geometric series, I $\log_{10}$-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) or food treatment on aggressive radius and growth rate. If the interaction between dominance status and food treatment was significant it was 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 the aggressive radius. Thus, I reported the results of the two-way ANCOVA in the section on aggressive radius. Finally, I used a multiple regression analysis to determine whether behavioural variables such as aggressive rate and aggressive radius influenced the growth rate of dominant and subordinate fish in this experiment once food treatment had already been entered into the model. 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 stream channel. Within a day, a dominant fish typically moved upstream and aggressively defended an area of the stream channel directly downstream of the feeder (Fig. 1). Subordinate territorial individuals 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 tended to be initially larger than subordinates, this difference was not significant (two-way ANOVA: $F_{1, 48} = 2.65$, $P = 0.11$); there was also no significant difference in initial mass of fish across food treatments (two-way ANOVA: $F_{5, 48} = 1.68$, $P = 0.158$).

The dominant fish foraged mainly in the forward direction, in the immediate area where food dropped from the feeder, but typically defended a large area of the stream channel. When food was scarce, the dominant fish easily monopolized the available food and confined the subordinate individuals to the downstream end of the stream channel (Fig. 1). When food abundance was intermediate, more subordinate individuals moved upstream and darted into the dominant's defended area to catch food items as they fell from the feeder (Fig.1). Dominant fish defended a smaller area and chased more often to exclude subordinates from the area downstream of the feeder. When food was abundant, most subordinate fish moved upstream to establish feeding stations immediately downstream from the feeder (Fig. 1).

Aggressive behaviour

The total number of aggressive acts over the course of the 15-minute observation period differed significantly across the food treatments (Fig. 2a; ANOVA: $F_{5,24} = 11.10$, $P < 0.001$). The total rate of aggression initially increased with increasing food abundance and then declined when food was abundant, as indicated by a significant quadratic term in a polynomial regression after the linear term was first entered in the model ($t_{27} = -4.51$, $P < 0.001$). On average, the fish engaged in 130 aggressive acts per 15-minute observation during the 5% treatment, whereas aggression rate dropped to only 45 acts per 15 minutes when food was scarce (i.e. 0.63%) or abundant (i.e. 10 and 20%). Fish were satiated and did not eat all the food during the 10 and 20% treatments.

The dome-shaped pattern of total aggression was related to two other measures of aggression. The percentage of individuals engaging in aggression also differed among food treatments (ANOVA: $F_{5,24} = 4.70$, $P = 0.004$). About 40% of individuals were aggressive at low and high levels of food abundance compared to 60-70% at intermediate levels of food abundance (Fig. 2b). Such a relationship was confirmed by a significant quadratic term in a polynomial regression ($t_{27} = -3.18$, $P = 0.004$). The per capita rate of aggression by the aggressive fish also differed significantly among the levels of food abundance (ANOVA: $F_{5,24} = 11.03$, $P < 0.001$). As with the other measures, the per capita rate of aggression initially increased with increasing food abundance, peaked at intermediate level of food abundance, and then decreased (Fig. 2c). This dome-shaped relationship between the rate of territorial aggression and the food abundance was supported by a significant quadratic term in a polynomial regression ($t_{27} = -4.92$, $P < 0.001$).

Aggressive radius

Water temperature had a significant positive effect on aggressive radius (two-way ANCOVA: $F_{1, 43} = 10.07$, $P = 0.003$), and hence was included as a covariate in all analyses. Mean aggressive radius of the focal fish differed significantly across food treatments (two-way ANCOVA: $F_{5, 43} = 3.46$, $P = 0.01$) and decreased with increasing food abundance for both dominant and subordinate fish (Fig. 3; two-way ANCOVA, linear contrast: $P = 0.005$). Overall, dominant fish had a larger aggressive radius than subordinate fish (two-way ANCOVA: $F_{1, 43} = 12.50$, $P = 0.001$). There was no significant interaction between food abundance and status (two-way ANCOVA: $F_{5, 43} = 0.27$, $P = 0.929$).

Growth

The mean specific growth rate of the focal fish over the course of the seven-day trials differed significantly across all food treatments (ANOVA: $F_{5, 24} = 113.38$, $P < 0.001$) and increased with increasing food abundance (Fig. 4a; ANOVA: linear contrast: $F_{1, 24} = 516.58$, $P < 0.001$). Curiously, the growth rate of the focal fish appeared to decline at the highest level of food abundance (Fig. 4a), but the difference between the 10 and 20% food treatments was not significant (Tukey post hoc test: $P = 0.437$).

As food abundance increased, the growth rate of all subordinates increased at a faster rate than dominant individuals as indicated by a significant interaction between dominance status and food treatment (Fig. 4b; two- way ANOVA: $F_{5, 48} = 19. 56$, $P < 0.001$). In spite of the significant interaction, the specific growth rate of focal fish increased with increasing food abundance for both dominant (ANOVA, linear contrast: $F_{1, 24} = 10.05$, $P = 0.004$) and all subordinate individuals (ANOVA, linear contrast: $F_{1,24} = 504.20$, $P < 0.001$). As noted before, growth rate appeared to decline at the highest food level, but the difference between the 10 and 20% treatments was not significant (Tukey post hoc tests: dominant fish: $P = 0.966$; subordinate fish: $P = 0.422$). Dominant fish grew faster than subordinate individuals in all food treatments except the 10 (Tukey post hoc test: $P = 0.998$) and 20% (Tukey post hoc test: $P = 0.999$) treatments.

Subordinate fish were further divided into two social categories: aggressive individuals, those with at least one aggressive act; and non-aggressive fish, those with no aggressive acts over the course of the 15-minute observation period. Aggressive subordinates had higher growth rates than non-aggressive fish (Fig. 4b; two-way ANOVA: $F_{1,47} = 13.30$, $P = 0.001$), but a post-hoc Tukey test indicated that this difference was only significant for the 2.5% treatment ($P = 0.004$). Moreover, growth rate of aggressive subordinates increased at a faster rate than non-aggressive individuals as indicated by a significant interaction between social status and food treatment (Fig. 4b; two-way ANOVA: $F_{5,47} = 3.60$, $P = 0.008$). The growth rate of non-aggressive subordinates increased at a slow rate with increasing food abundance when food was scarce and abundant, but increased at a faster rate when food was at an intermediate level of abundance (Fig. 4b). The relationship between specific growth rate of subordinates and food abundance was supported by significant cubic terms in a polynomial contrast for both aggressive ($F_{1,24} = 20.40$, $P < 0.001$) and non-aggressive ($F_{1,23} = 30.66$, $P < 0.001$) individuals.

Predictors of growth rate

A multiple regression analysis was used to determine which behavioral variables (aggressive rate and aggressive radius) influenced the growth rate of fish in this experiment, in addition to food abundance. Growth rate of dominant fish increased significantly with dominant aggressive rate, but not dominant chase radius (Table 1). Food treatment and aggressive rate combined accounted for approximately 35% of the variation in specific growth rate among dominant individuals. No behavioral variable had a significant effect on the growth rate of the average subordinate fish after food treatment was entered into the model (Table 1). Food treatment accounted for almost 89% of the variation in growth rate among subordinate fish.

Territory size versus food abundances

I compared the effect of food abundance on territory size in my study to that of Slaney and Northcote (1974) and Keeley (2000); both studies introduced young rainbow trout to three levels of food abundance (Fig. 5). For the purpose of comparison, territory size and food abundance were transformed to multiples of the mean territory size and food abundance for each study, respectively.

Like previous studies, territory size in my study changed inversely with food abundance (Fig. 5), confirming the prediction of models of optimal territory size (Schoener 1983). However, the relationship in my study had a shallower slope compared to those of Slaney and Northcote (1974), Keeley (2000), and a synthesis of data in Grant et al. (1998) (Fig. 6). Note that the mean slopes in the other studies were all outside of the 95% C.I. about the slope in my analysis. All the observed slopes were shallower than the slope of -1.0 suggesting that territory size changes less than one would expect if fish were maintaining a constant amount of food in their territories (Fig. 6).

Discussion

Dominance hierarchies

Dominance hierarchies occur in group foraging animals due to variation in the relative competitive abilities of individuals (Huntingford and Turner 1987). Dominant individuals often occupy the most profitable feeding sites and hence grow larger than subordinates (Fausch 1984; Huntingford et al. 1990). As expected, in my experiment the dominant individuals occupied a central upstream foraging station, directly under the feeder, and had a priority of access to food items as they fell from the feeder. In previous studies on social fish groups, such as fairy basslet (*Gramma loreto*) and sponge-dwelling cleaning gobies (*Elacatinus prochilos*), body size was strongly correlated with dominance status (Webster and Hixon 2000; Whiteman and Côté 2004). However, in my study dominant fish were not initially always the largest individual. Nevertheless, the dominant individuals had a larger aggressive radius and a higher growth rate than subordinates over the course of the experiment. Consistent with my results, Thorpe et al. (1992) reported that dominant status of juvenile Atlantic salmon is more influenced by an individual's aggression than its size. Thus, body size can be the effect of dominance and not its cause (Huntingford et al. 1990).

Not surprisingly, the specific growth rate of focal fish increased with increasing food abundance and tended to level off when food was superabundant. Dominant fish often have a higher growth rate than subordinates (Yamagishi 1962; Brown 1964; Li and Brocksen 1977), mainly due to differential access to food: dominant fish defend the most profitable feeding sites (Yamagishi 1962) and thus, interfere with the feeding of subordinates. 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 and Dill 1989; Lee et al. 2011). In my experiment, the dominant fish had a higher growth rate than subordinates when food was limited and grew at the same rate as aggressive and non-aggressive subordinates when food was in excess. Brännäs et al. (2003) also reported a difference in growth rate of juvenile brown trout (*Salmo trutta*) due to differences in social status. Nonetheless, when food was superabundant in their experiment, aggressive and non-aggressive individuals grew at the same rate as the dominant fish. At low levels of food abundance, dominant fish, in my experiment, easily monopolized the available food and excluded subordinates to the downstream corners of the channels. As food abundance increased, dominant fish may have been constrained by handling time and were thus unable to monopolize the food items that dropped from the feeder, leaving more food available for subordinates. When food was superabundant, aggressive and non-aggressive individuals had access to the same amount of food as the dominant fish. Consistent with the results of Brännäs et al. (2003) the difference in growth rate of aggressive and non-aggressive individuals was highest at intermediate food levels whereas similar growth rates were observed at the highest and lowest food levels.

Aggressive rate was a significant predictor of dominant growth rate in my experiment. By increasing their chase rate, dominant fish may have increased their access to food by excluding more subordinates from the food source. No behavioural variables were significant independent predictors of subordinate growth rate. Not surprisingly, food treatment accounted for most of variation in growth rate of dominant and subordinate individuals.

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 and reduce food monopolization by dominants (Basquill and Grant 1998; Sundbaum and Naslund 1998). Höjesjö et al. (2004) showed that increased habitat complexity reduces the growth advantage of dominant individuals compared to subordinates. In complex habitats, aggressive fish may not be able to monopolize food as efficiently due to a decrease in their ability to detect (Savino and Stein 1982) and chase intruders (Stamps 1984). Hence, the benefits of defense may not exceed the increased costs of defense, such as a higher metabolic rate (Metcalfe et al. 1995) or an increased predation risk (Jakobsson et al. 1995), in complex habitats. Therefore, the difference between dominants and subordinates in my experiment may be less extreme in a natural stream.

Aggressive behavior

Food was presented in an economically defendable (Brown 1964) manner in my experiment. The food dropped into the water in a small area of the channel below the feeder and was dispersed over the 12-hour period of "daylight". Hence, the food was predictable in space, clumped in space, and dispersed in time; all three characteristics promote defendability of the resource (Grant 1993). Thus, it was not surprising that some individuals defended feeding territories in all trials.

As predicted by the threshold model of territoriality, there was a dome-shaped relationship between the frequency and intensity of aggression and food abundance, indicating that fish modified their aggressive behaviour to conspecifics in response to changes in food abundance.

As mentioned in the Introduction, many studies show a decrease in aggression when food is superabundant (i.e. Magnuson 1962; Slaney and Northcote 1974), mainly due to satiation. However, in natural streams 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 (i.e. caused by heavy rainfall or an emergence of insects; Waters 1965) 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 and Yamamoto 1962; Newman 1965). The only other study to document a dome-shaped relationship between aggression and food abundance also used a broad range of food abundance, from 12.5 to 300% of what fish could eat (Grant et al. 2002).

Aggressive radius and defended area

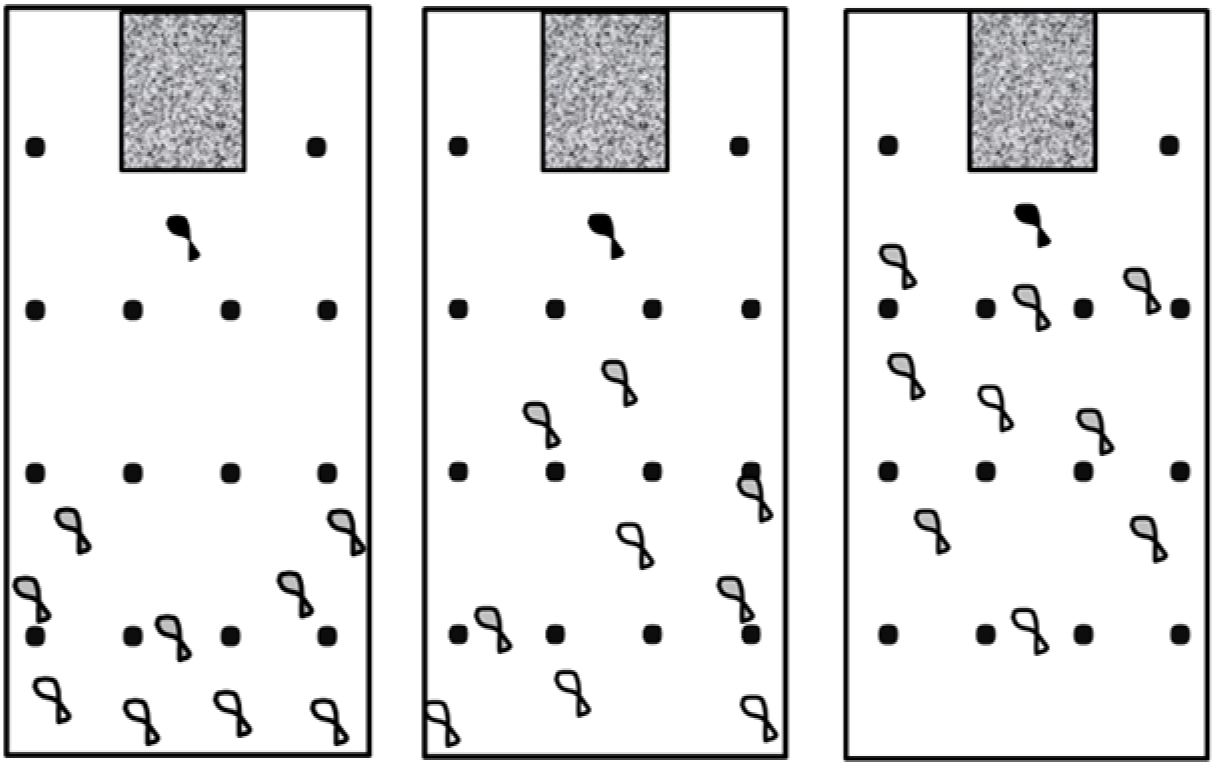
When food abundance was low, dominant fish were able to defend a large area of the stream channel and confined subordinate individuals to the downstream corner of the channel. Dominant fish may have devoted the time between the arrival of food items to the intimidation of subordinate individuals. Hence, dominant fish may have defended as large a territory as possible to discourage intruders from stealing food items (Praw and Grant 1999). However, as food abundance increased, dominant fish may have been constrained by processing food items and thus may have dedicated less time to intimidating subordinates. Therefore, individual costs to subordinates such as injuries or stress associated with aggressive interactions may have been reduced, causing more subordinates to enter the dominant's foraging area and catch food items as they fell from the feeder (see also Praw and Grant 1999).

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 15% 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). In addition, Slaney and Northcote (1974) and Keeley (2000) reported a decrease in territory size of juvenile rainbow trout, with increasing food abundance, with a steeper slope than my study. The steeper slopes in previous studies compared to mine may have been related to emigration; fish were allowed to emigrate which resulted in a decrease in fish density when food abundance was low. Thus, changes in territory size were caused by changes in both the intruder pressure and food abundance. By contrast, in my study the fish density was held constant and changes in territory size were the result of changes in food abundance alone. Nonetheless, in all experiments, territory size decreased with a much shallower slope than one would expect if fish were maintaining a constant supply of food on their territories, suggesting that an increase in food abundance would have a small effect on territory size and thus on density of juvenile salmonids.

Implications

My study supported the prediction of the threshold model of territoriality – a dome-shaped relation between the frequency and intensity of aggression and food abundance (Brown 1964) – which had not been previously documented in juvenile stream-dwelling salmonids. The results of my experiment may be useful in adjusting feeding regimes in salmonid hatcheries, where the goal is to maximize growth rate while minimizing aggression and differences in body size between individuals (Thorpe and Huntingford 1992). Excess food (i.e. 10% treatment) can maximize growth rate and decrease aggression by increasing satiation, but uneaten food often lowers the quality of water and wastes resources. Maximum growth rate can still occur when fish are fed just to satiation (i.e. 5% treatment). In order to minimize aggression, food should be presented in an undefendable manner: temporally clumped, spatially dispersed, and spatially unpredictable. To achieve this goal, the daily ration of food should be divided into a number of small portions and delivered at random times and locations throughout the day. In order to present food in a spatially dispersed manner, the food can be spread evenly over the surface of the water.

The results of this experiment quantified the relationship between territory size and food abundance over a broader range of food abundance than in previous studies. However, a 32-fold increase in food abundance caused territories to shrink to only 50% of their initial size. Stream fertilization has been considered as a habitat management option to increase salmonid abundance in nutrient deficient streams (Slaney et al. 1994). However, the results of my experiment suggest that, an increase in food abundance would have a relatively small effect on territory size and thus on fish population density (Grant et al. 1998). Nonetheless, a 32-fold increase in food abundance in my experiment, caused the growth rate to increase to 9 times its initial value, suggesting an increase in food abundance may increase salmonid abundance by affecting the individual growth rate rather than the population density. Concurring with my results, a review of four stream fertilization experiments by 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 age at smoltification (Hutchings and Jones 1998) and hence, increase smolt production (e.g. Slaney and Ward 1993). However, an increased growth rate can cause a higher proportion of sexually mature male parr (Hutchings and Jones 1998), which may reduce the number of anadomous males returning to spawn. Hence, any attempt to enhance salmonid population by increasing the productivity of the stream should carefully consider the potential benefits and costs of increased food abundance.



Low Food Medium Food High Food

Figure 1. Representation of the space use by three types of fish at different levels of food abundance: dominant fish ( ), aggressive subordinates ( ), and non-aggressive subordinates ( ). Black circles show the position of cobbles in the stream channel and the grey squares indicate the position of the feeder.

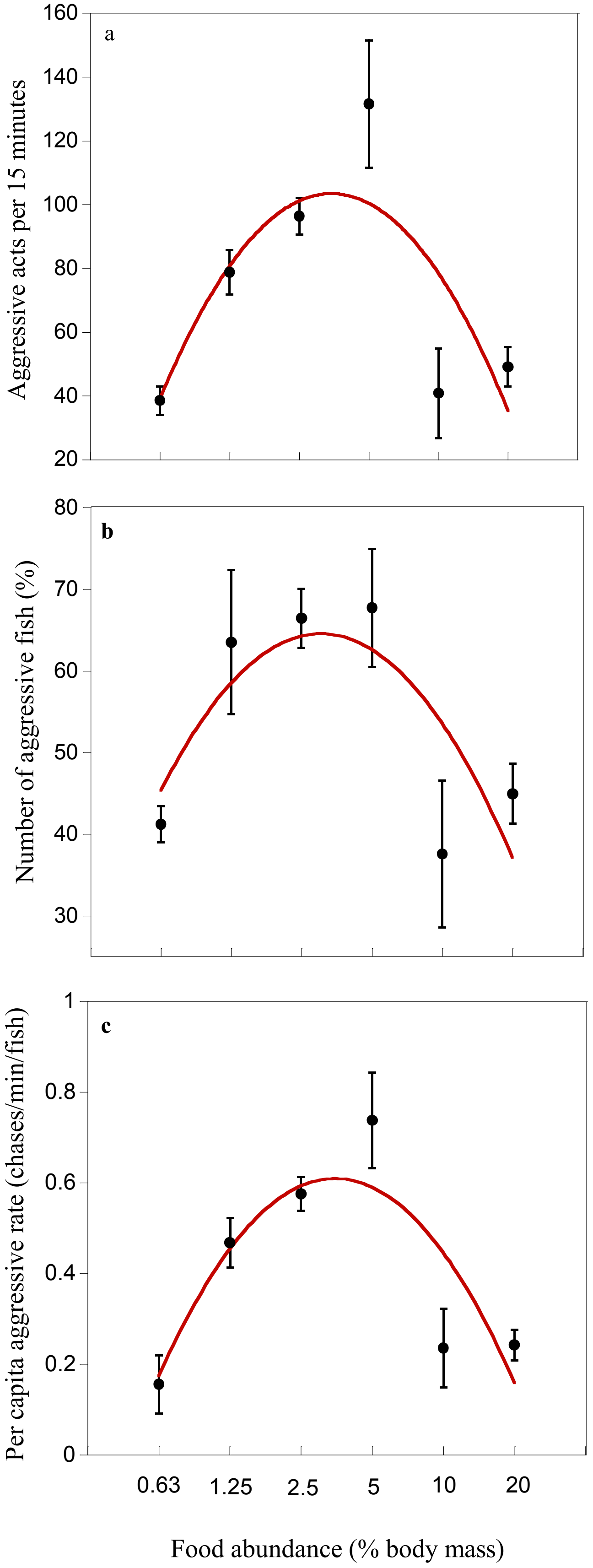


Figure 2. Effect of food abundance on mean (± SE, N = 5) (a) number of aggressive acts ($Y = -117.36\ X^2 + 126.57X\ + 69.37$, $F_{2,\,27}$ = 10.18, $r^2 = 0.43$, $P < 0.001$), (b) proportion of aggressive individuals ($Y = -40.96\ X^2 + 39.52X + 55$, $F_{2,\,27} = 5.53$, $r^2 = 0.29$, $P = 0.009$), and (c) per capita aggressive rate of aggressive fish (chases/fish/min) ($Y = -0.71X^2 + 0.74\ X – 0.41$, $F_{2,\,27} = 12.38$, $r^2 = 0.48$, $P < 0.001$). The solid lines represent the quadratic regressions. Note the logarithmic scale on the x-axis.

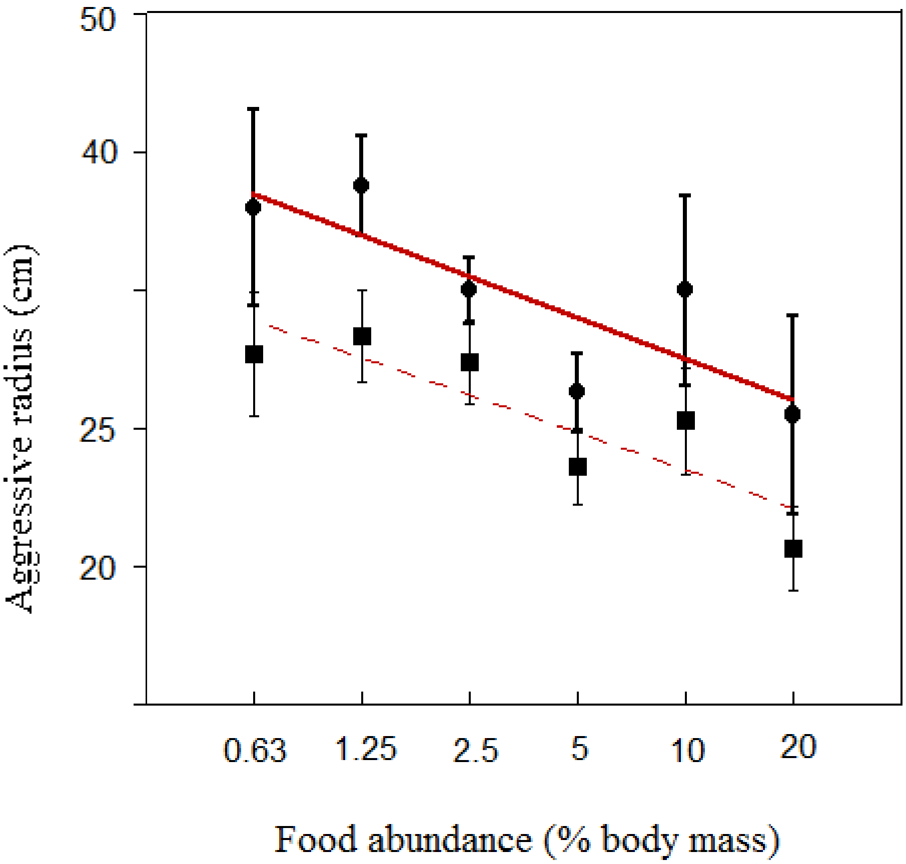


Figure 3. Mean (± SE, N = 5) aggressive radius of dominant (●) and aggressive subordinate fish (■) in relation to food abundance. The lines represent linear regressions (solid line: Y = -0.10X + 1.55, r^2 = 0.19; dotted line: Y = -0.11X + 1.46, r^2 = 0.26). Note that N = 3 for 0.63% treatment since the dominant fish did not show any aggressive behaviour in 2 of the trials. Note the logarithmic scale on both the axes.

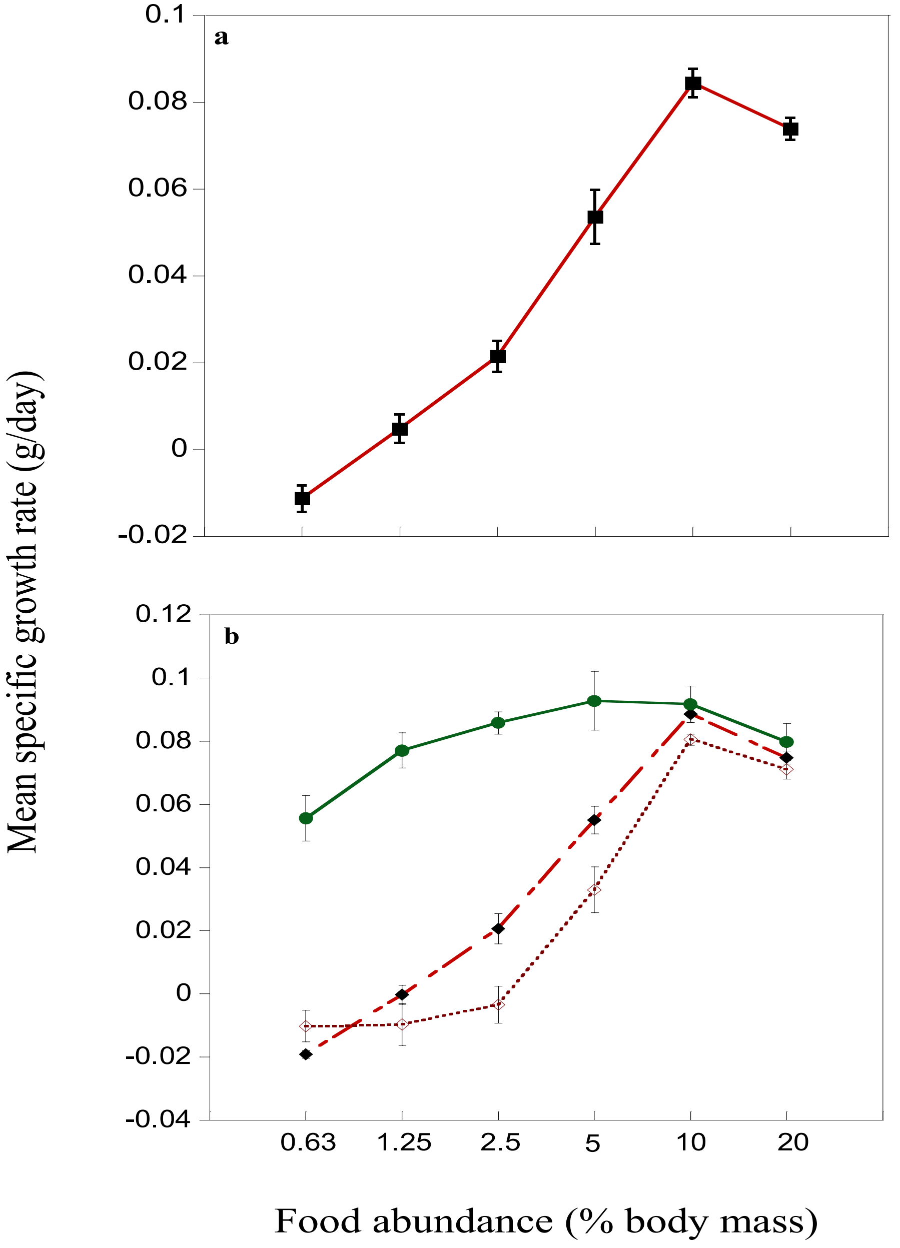


Figure 4. Effect of food abundance on mean (± SE, N = 5) specific growth rate of (a) focal fish and (b) dominant fish (●), the average aggressive subordinate fish (♦), and the average non-aggressive subordinate fish (◊) in relation to food abundance. Note the logarithmic scale on the x-axis.

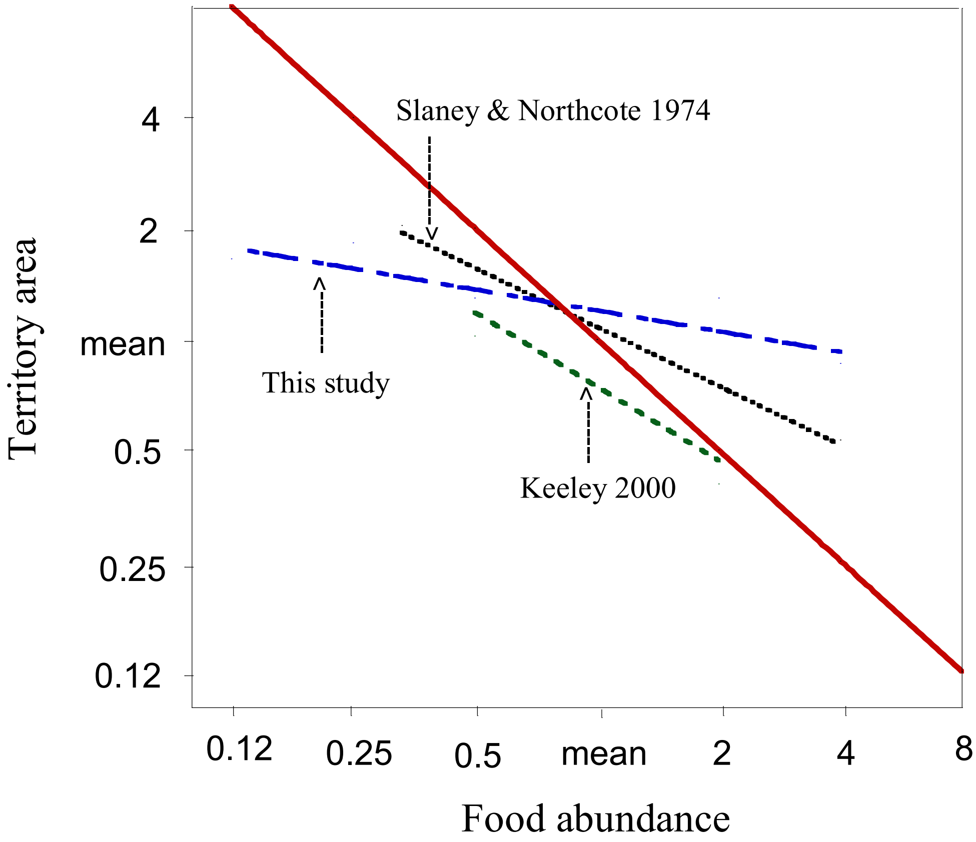


Figure 5. Effect of food abundance (multiples of the mean) on territory size (multiples of the mean). The solid line is the predicted territory size if fish defend a constant amount of food. Note the logarithmic scale on the axes.

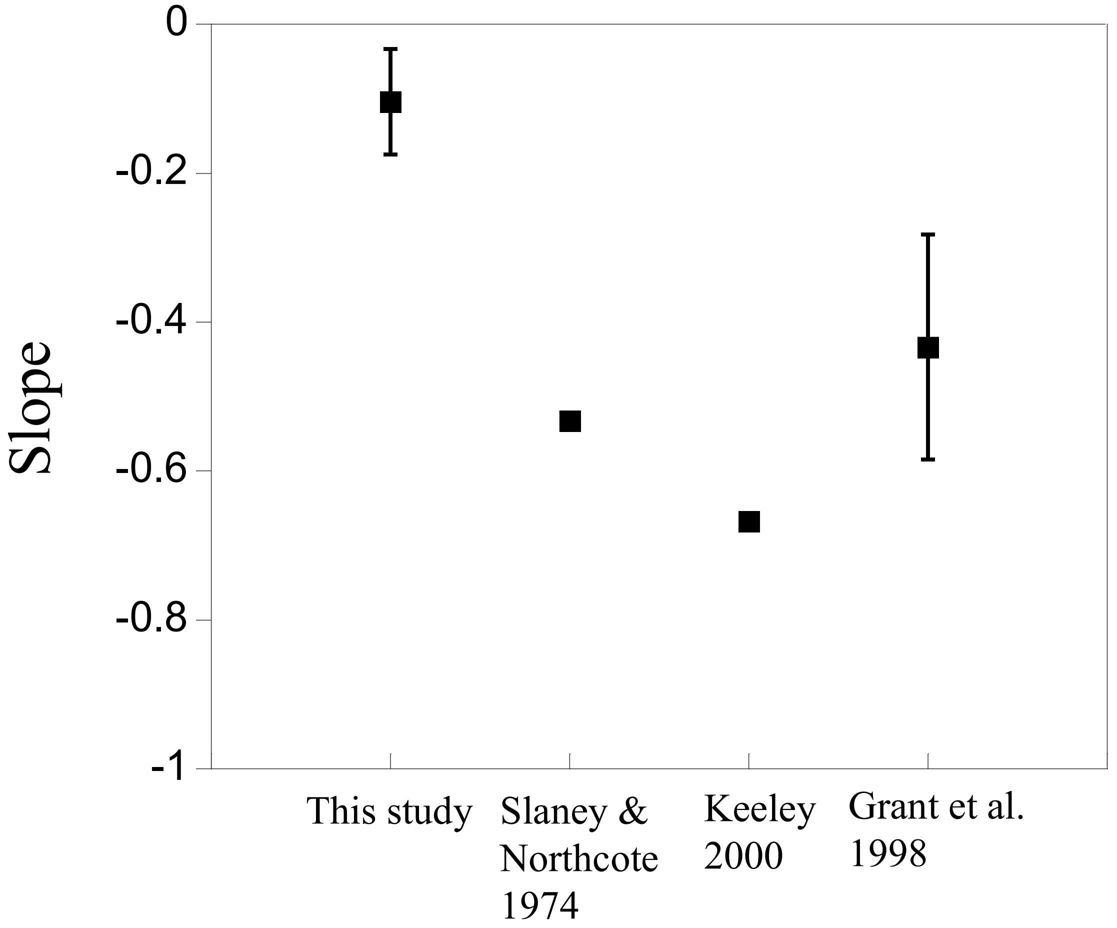


Figure 6. Comparison of the mean (■) and 95% C.I. of the slope of the least squares regression of the territory size versus food abundance relationship in four studies.

Table 1. Predictors of growth rate of dominant and subordinate fish from a multiple regression analysis.

Variable	**Dominant fish**			**Subordinate fish**		
	***b**	**T**	**P**	***b**	**T**	**P**
Food abundance	0.45	2.93	0.007**	0.95	13.84	0.000**
Aggressive rate (chases/min)	0.36	2.33	0.028**	0.053	0.837	0.41**
Aggressive radius	0.092	0.47	0.644	-0.02	-0.35	0.728

Note: * Partial regression coefficient from a multiple regression analysis. ** P-values when aggressive radius was removed from the model.

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