

The costs and benefits of territory sharing for the Caribbean coral reef fish, *Scarus iserti*

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Summary. Along the Caribbean coast of Panama, groups of unrelated female striped parrotfish, *Scarus iserti*, co-defend a common feeding territory. Field manipulations of group size and composition were performed to examine the benefits and costs accrued by dominant fish within these shared territories. Dominant fish benefit from the presence of relatively large subordinates because they share in the defense of the territory. Removals of these fish caused increases in defense time and decreases in feeding time for dominant group members. Dominants benefit from the presence of small subordinates because they increase the foraging efficiency of dominants. Removals of smaller subordinates caused reductions in the feeding time of dominant fish, although no changes in defense time occurred. Concurrently, dominant fish reduce costs of resource depletion by displacing subordinate group members from good food patches. Dominance interactions within a group reduce the amount of time subordinates spend feeding (subordinate individuals fed at higher rates following the removal of a dominant) and limit a subordinate's access to high quality resources. This combination of benefits and reduced costs ultimately contributes to the economic defensibility of a striped parrotfish territory and has led to the evolution of group territorial behavior in the absence of kin selection and cooperative parental care.

Introduction

The concept of "economically defensible" resources was originally proposed to explain the territorial defense of an exclusive area by a solitary

individual (Brown 1964). Based on optimality principles, it predicts that territorial behavior may evolve when the benefits an individual receives from enhanced access to a protected resource outweigh the costs of defending that resource. Within the last two decades, numerous empirical studies of territories defended by solitary individuals have provided general support for this idea (e.g., Gill and Wolf 1975; Carpenter and MacMillen 1976; Myers et al. 1979; Pyke 1979; Carpenter et al. 1983; McFarland 1986; Hart 1987; Mares and Lacher 1987; Temeles 1987; Ydenberg and Krebs 1987).

More recently, the concept has been extended to help explain the evolution of group territoriality, the joint defense of an area by more than one individual. This behavior is generally expressed among socially cooperative groups of either birds or mammals. Studies of these groups have demonstrated that a variety of different environmental and ecological factors may contribute to the economic defensibility of shared territories, although any of three conditions, in particular, are often deemed sufficient for their development. These are: extreme costs to the dispersal of offspring from a territory (Brown 1974, 1978, 1982; Gaston 1978; Emlen 1982, 1984; Koford et al. 1986; Lindström 1986), cooperative care of young within the territory (Brown 1974, 1982; Gaston 1978; Vehrencamp 1977, 1978; Woolfenden and Fitzpatrick 1978, 1984; Emlen 1982, 1984), and kin selection among group members (Brown 1974, 1982; Koenig and Pitelka 1981; Emlen 1984; Lindström 1986).

None of these factors, however, can account for the group territorial behavior of the Caribbean striped parrotfish, *Scarus iserti*. Female groups of these fish co-defend a common feeding territory from neighboring territorial and roving non-territorial conspecifics (Buckman and Ogden 1973;

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Clifton 1989). Group members are unrelated to each other (juveniles recruit onto a reef only after an approximately month-long planktonic egg and larval stage), and they spawn their eggs directly into the water column with no subsequent parental care. Thus, the territorial behavior of these fish presents an intriguing contrast to the more typical patterns of territory sharing mentioned above and offers a unique opportunity to explore the costs and benefits of group territorial behavior in the absence of kin selection and cooperative care of young.

This paper examines striped parrotfish group territoriality, reporting on how behaviors and resources shift following experimental manipulations of group size and composition. The results quantify the extent to which specific aspects of group territorial existence influence individual food intake rates and, in the process, identify the factors contributing to the economic defensibility of these territories. Of particular interest are the specific ways in which social rank within a group influences individual payoffs. The findings presented here indicate that size-related differences in competitive ability among group members have played a critical role in the evolutionary development of striped parrotfish group territorial behavior.

Methods

Subject animal

The striped parrotfish is a common Caribbean coral reef fish. A protogynous hermaphrodite with two distinct color phases (Randall 1983), these small herbivores (maximum size 15 cm; all measures of fish are standard length, S.L.) spend much of their time scraping microalgae and benthic diatoms from the bottom with their beak-like mouths. Striped parrotfish are found in a variety of social contexts (e.g., territorial groups, foraging schools, mating aggregations, etc.) and have been the subject of many behavioral studies, including work on their foraging strategies (Ogden and Buckman 1973; Barlow 1975; Robertson et al. 1976), mating and life history tactics (Randall and Randall 1963; Warner and Downs 1977; Robertson and Warner 1978), and territorial behavior (Buckman and Ogden 1973; Clifton 1989).

Up to eight females jointly defend algal food resources from conspecific intruders. This food grows throughout a territory as a scant, filmy cover on dead coral rubble and sand. Algal density at a particular site is, in part, a function of the time since an area was last grazed, and fish do not harvest these resources systematically. Thus, unlike many other coral reef fish territories (e.g., damselfish, *Stegastes spp.*), resources are not uniformly distributed within a territory. Instead they may be found as ephemeral patches that vary unpredictably in location through time.

A size-related dominance hierarchy is present within each group, and larger individuals displace smaller group members during bouts of feeding. All group members participate in the defense of a territory; however, their relative contribution to

defense is quite variable. Three classes of territorial individuals have been identified: small subordinates (less than 6.5 cm) that defend only rarely, larger subordinates that generally contribute a great deal to the defense of a territory, and the dominant group member whose contribution to defense depends upon group composition. More detailed accounts of this territorial behavior are described elsewhere (Buckman and Ogden 1973; Clifton 1989).

These fish are excellent subjects for time budget studies. They readily habituate to the presence of a diver, and their various behaviors are easily distinguishable. In addition, female striped parrotfish, with their indeterminate growth, daily spawning, and sex-changing life history pattern, are presumably energy maximizers (*sensu* Schoener 1971), since any net gain in energy can be immediately converted into either increased egg production or growth, both major contributors to life-time reproductive success (Warner and Downs 1977; Robertson and Warner 1978). Thus, there is probably strong selection for minimizing the amount of time spent away from feeding.

Territorial striped parrotfish were studied during visits to the Smithsonian Tropical Research Institute field station, located among the San Blas islands off the Caribbean coast of Panama. Observations of these fish were made over an approximate 2-year period (March-September 1984; April-August 1985; March-April 1986). Time budgets of territorial individuals were collected during 5 min bouts of observation using an underwater tape recorder and subsequently transcribed with an event-recording portable computer. During observation periods, the time the focal animal spent feeding, defending the territory, displacing and being displaced by other group members, swimming within the territory, and swimming off territory were noted. During interactions with other individuals, the identity and size of the individual were also noted. Individuals were individually recognizable by means of uniquely applied patterns of subcutaneous injections of the vital stain Alcian Blue.

Removal experiments

Experiments were performed in a pair-wise fashion, using two territorial groups on the same reef. Paired groups were of the same size (either three or four individuals) and relatively equivalent in composition. To obtain individual behavior profiles, fish from both groups were simultaneously monitored each day, over a period of at least 5 days. All observations were made within the same block of time each day, during which each group member was monitored separately for a 5-min period. The sequential order in which fish were observed from day to day was varied systematically.

Following this pre-manipulation period, a specific individual was removed from one of the territories (chosen randomly and hence referred to as the "experimental" territory). This removal was done approximately 30 min before the usual period of observation. A mock removal was performed in the second territory (hence referred to as the "control" territory), matching the removal procedure used in the experimental territory, except that no fish was removed. After a 15-min wait, all remaining fish were observed in both of the territories, as they were on subsequent days, for at least 4 more days.

Behaviors of experimental fish before and after a removal were compared with a repeated measures ANOVA design. All variables were arcsine transformed and only three of six possible behaviors were used in the analysis. This reduced potential problems of dependence between behavior categories (Aitchison 1982). The behavior of the control fish was included as an additional independent variable in these analyses. Statistical analyses were performed in this manner because, on a given

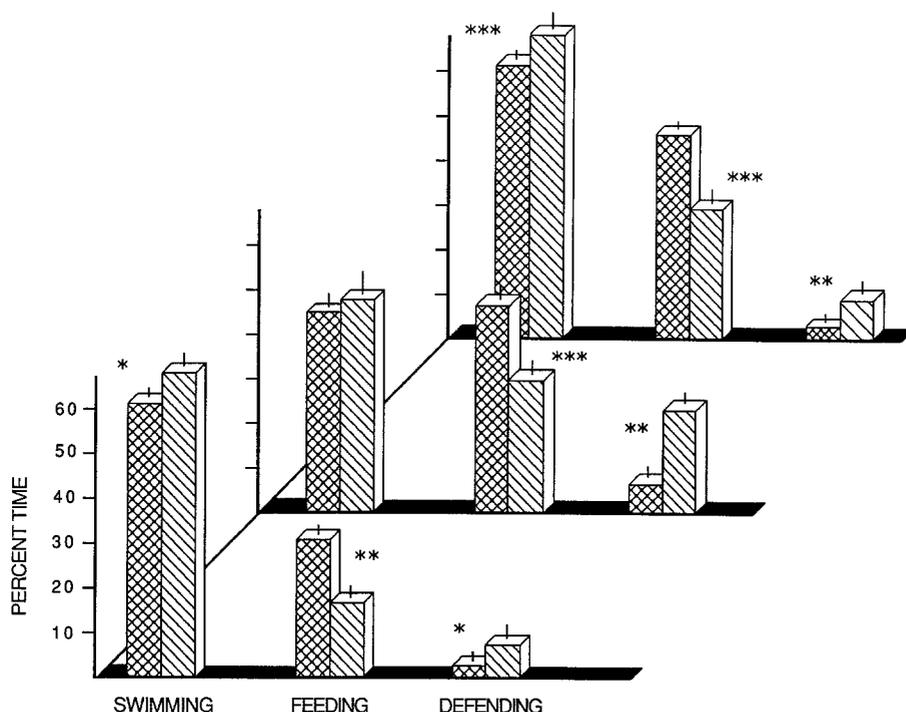


Fig. 1. Mean percent time spent swimming, feeding, and defending (± 1 SE) by three dominant territory residents before and after the removal of a contributing subordinate group member (see text for details). Double-hatched bars are pre-manipulation; single-hatched bars are post-manipulation. Repeated measure ANOVAs on arcsine transformed variables. Significance of changes in behaviors before and after the manipulation: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; otherwise $P > 0.05$

day, ambient conditions (e.g., water clarity, cloud cover, surge) generally affected striped parrotfish behavior so that the patterns of foraging among all territorial individuals on the same reef tended to covary. Thus, at least prior to the manipulation, the behavior of the control fish was a reasonable predictor of the behavior of the experimental fish.

Three types of removal experiments were performed, based upon the rate at which an individual contributed to the defense of a territory during the premanipulation period. In the first case, subordinate individuals that performed more than 50% of the total defense of an area were removed (hence referred to as "contributors"). In the second case, small subordinate group members that contributed less than 5% to the total defense of an area were removed (hence referred to as "non-contributors"). In the third case, large, dominant fish were removed from their territory, irrespective of their overall contribution to territorial defense. Both types of subordinate removals were replicated in three territories. A total of five dominant removals were performed.

To assess whether removals influenced a dominant's feeding efficiency, algal patches of known quality were introduced into several territories both before and after removals. The time until discovery of these patches by the dominant group member was then recorded. Patches were small pieces of relatively high quality algal turf (approximately 3×3 cm; mean algal density = $8.7 \times 10^{-2} \pm 2.1 \times 10^{-3}$ mg/cm²; $N=7$; all means ± 1 SE) collected from nearby damselfish territories. During one non-contributor removal and one contributor removal, a single piece of turf was placed at an arbitrary location within both experimental and control territories. This was done each day of the experiment, just after the main observation period. A patch was considered discovered when the dominant began to feed on the introduced algae.

Algal density within territories was estimated from samples scraped from unglazed ceramic tiles (2.6×2.6 cm) that had been left, unmanipulated, within the territory for at least 45 days prior to any experiments. Samples were preserved in 10% buffered formalin immediately following collection and were later

ashed to obtain ash-free dry weights. Algal samples collected in this manner provide accurate estimates of actual algal densities within territories (Clifton 1989).

Two types of tile collection schemes were used during the experiments. In the first, three sets of two tiles each were placed at three different locations within three of the experimental territories (two in which a non-contributing subordinate was removed and one in which a contributing subordinate was removed). One tile from each set was collected just prior to the removal, and the second was collected 5 days after the removal. In the second collection scheme, tiles were arranged in sets of 15 (laid out in a 3×5 pattern) and placed at five arbitrarily chosen locations within one of each type of experimental territory. Tiles were similarly distributed in the associated control territories. After being left unmanipulated for at least 45 days (as above), three randomly chosen tiles from each set within both experimental and control territories were collected just prior to the removal. A similar collection of three tiles from each set was made following the last post-manipulation observation period.

Results

Removal of subordinate defenders

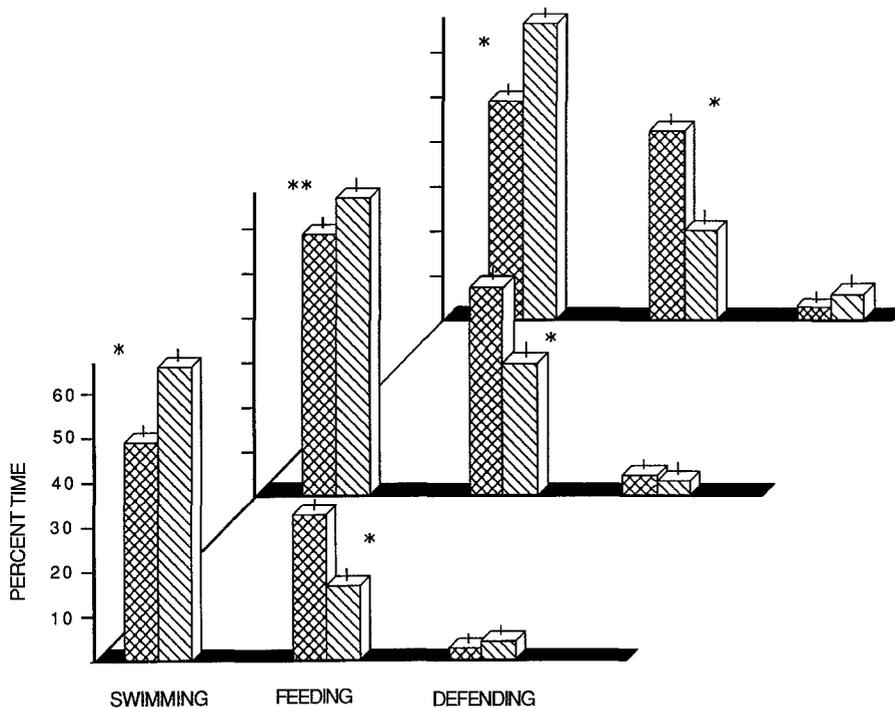
The removal of a contributing subordinate severely affected the largest group member's behavior (Fig. 1). Following each of the three removals of this type, there was a reduction in the amount of time the dominant group member spent feeding ($\bar{x} = 16.3 \pm 2.2\%$) and an increase in the amount of time it spent defending the territory ($\bar{x} = 10.5 \pm 3.8\%$). In two of the three removals, the amount of time spent swimming also increased ($\bar{x} = 9.5 \pm 4.5\%$). Changes in algal density within territories

Table 1. Mean algal density (mg/cm²) from three experimental territories before and after the removal of a subordinate; *N*=6 for each. All weights are ash-free

Type of removal	Before	After	<i>t</i>	<i>P</i>
Contributor	$1.2 \times 10^{-2} \pm 2.3 \times 10^{-3}$	$1.3 \times 10^{-2} \pm 1.3 \times 10^{-3}$	0.45	0.69
Non-contributor	$1.8 \times 10^{-2} \pm 3.7 \times 10^{-3}$	$1.9 \times 10^{-2} \pm 1.0 \times 10^{-3}$	0.32	0.78
Non-contributor	$2.3 \times 10^{-2} \pm 1.9 \times 10^{-3}$	$2.0 \times 10^{-2} \pm 1.3 \times 10^{-3}$	4.41	0.06

Table 2. Mean algal densities (mg/cm²) from three experimental and three control territories before and after removal of a subordinate group member. All measures from ash-free samples. Sites within territories are pooled

Type of removal	Before	After	<i>F</i> _{1,29}	<i>P</i>
Non-contributor (control)	$1.3 \times 10^{-2} \pm 6.8 \times 10^{-4}$ $2.5 \times 10^{-2} \pm 1.9 \times 10^{-3}$	$1.2 \times 10^{-2} \pm 7.4 \times 10^{-4}$ $2.4 \times 10^{-2} \pm 1.4 \times 10^{-3}$	0.27 0.52	0.62 0.49
Contributor (control)	$2.7 \times 10^{-2} \pm 2.2 \times 10^{-3}$ $2.2 \times 10^{-2} \pm 1.7 \times 10^{-3}$	$2.4 \times 10^{-3} \pm 2.0 \times 10^{-3}$ $2.3 \times 10^{-3} \pm 1.3 \times 10^{-3}$	4.41 0.90	0.06 0.37
Dominant (control)	$2.5 \times 10^{-2} \pm 2.5 \times 10^{-3}$ $2.2 \times 10^{-2} \pm 1.3 \times 10^{-3}$	$2.3 \times 10^{-2} \pm 1.9 \times 10^{-3}$ $2.5 \times 10^{-2} \pm 1.7 \times 10^{-3}$	2.36 1.16	0.16 0.38

**Fig. 2.** Mean percent time spent swimming, feeding, and defending (± 1 SE) by three dominant territory residents before and after the removal of a non-contributing subordinate group member (see text for details). Bar hatching and significance levels as in Fig. 1

were not detected following the removals (Tables 1 and 2). In the experimental territory in which high quality food patches were introduced, the mean time until discovery of a patch by the dominant group member increased following the removal (from 75.4 ± 22.1 s to 154.4 ± 25.6 s; original group size = 4; *N* = 10; *t* = 2.33; *P* < 0.05). No such change was detected in the associated control territory (83.4 ± 21.2 s vs 65.2 ± 20.9 s; *N* = 10; *t* = 0.61; *P* = 0.56).

Removal of subordinate non-defenders

These experiments also affected the behavior of dominant territorial individuals (Fig. 2). In all three cases, the amount of time spent feeding declined significantly following the removal (\bar{x} = $18.0 \pm 3.6\%$), while the amount of time spent swimming increased significantly (\bar{x} = $18.6 \pm 1.9\%$). The removal of a non-contributing subordinate had no effect, however, upon the amount of

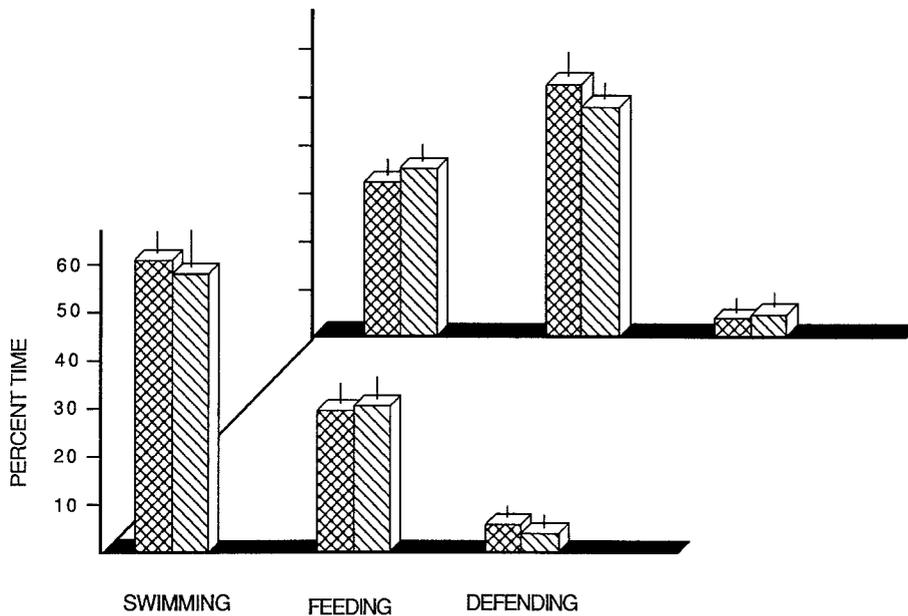


Fig. 3. Mean percent time spent swimming, feeding, and defending (± 1 SE) by two subordinate territory residents before and after the removal and subsequent replacement of the most dominant group member (see text for details). Bar hatching and significance levels as in Fig. 1

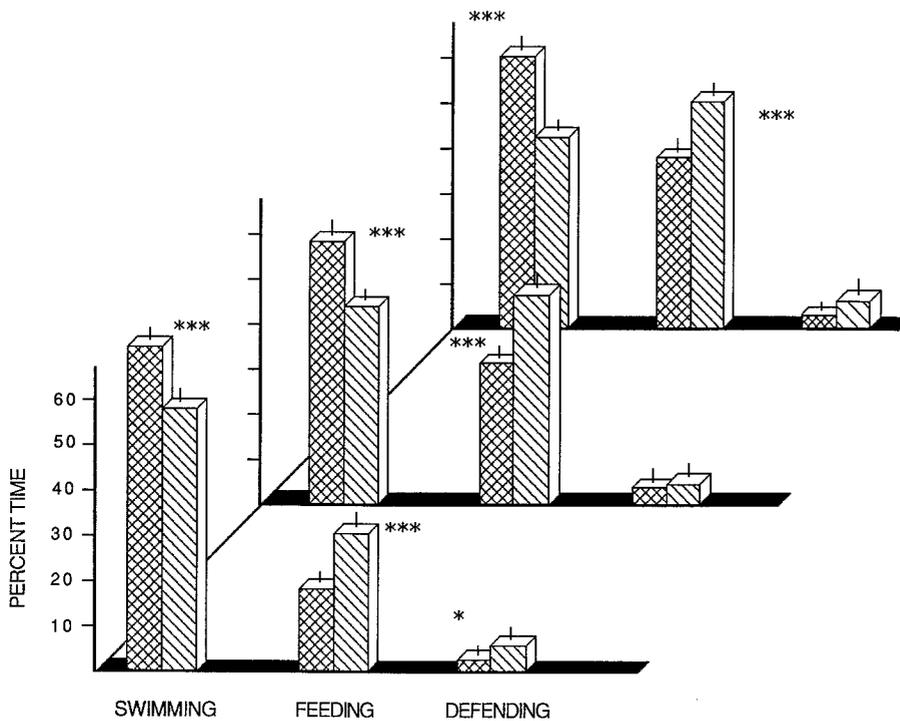


Fig. 4. Mean percent time spent swimming, feeding, and defending (± 1 SE) by three subordinate territory residents before and immediately after the removal of the most dominant group member (see text for details). Bar hatching and significance levels as in Fig. 1

time a dominant individual spent defending its territory. Algal densities were unaffected by the removal (Tables 1 and 2). As above, when high quality food patches were introduced into one of the experimental territories, the mean time until discovery by the dominant group member was higher following the removal (150.8 ± 27.4 s vs 277.8 ± 47.3 s; original group size = 3; $N = 10$; $t = 2.32$; $P < 0.05$). Again, the dominant fish in the associated control territory showed no change in

discovery rate (180.4 ± 31.6 s vs 169.4 ± 38.8 s $N = 10$; $t = 0.61$; $P = 0.56$).

Removal of a dominant group member

The most obvious result of removing a dominant fish from its territory was the subsequent invasion of the territory by a large neighboring territorial striped parrotfish. These fish then effectively occupied and defended both territories, which contin-

ued to be maintained separately by the two groups of smaller territorial individuals. In each case, these invaders were at least 1 cm larger than the largest of the remaining original residents of the experimental territory.

Both invasions occurred within 24 h of the removal. One took place 30 min following the removal and was directly observed. In this case, the original residents of the experimental territory initially defended the territory against the intrusions of a large neighbor. However, their defensive attempts were soon met with aggressive chases by the larger fish and were subsequently curtailed. Following the invasion of the territory, the behaviors of the largest remaining subordinate within the experimental territory were not different from the patterns of behavior expressed prior to the manipulation (Fig. 3). Algal densities within experimental and control territories were unchanged (Table 2).

Because the initial removals of a dominant territorial group member resulted in the invasion of the territory by large, neighboring fish, patterns of subordinate behavior in the presence and absence of a large dominant group member could not be analyzed. To alleviate this problem, the experimental procedure was modified so that five sets of 5-min bouts of observation were made immediately before and immediately following a removal. This new procedure was then repeated three times.

Following the removal of the largest group member, but prior to the invasion of the territory by a larger fish, the behavior of the largest remaining subordinate fish changed dramatically (Fig. 4). In each case, the amount of time the subordinate fish spent swimming significantly decreased ($\bar{x} = 16.2 \pm 1.9$), and the amount of time it spent feeding significantly increased ($\bar{x} = 16.7 \pm 1.6$). In one instance, the time spent defending the territory also increased significantly.

Discussion

Territorial behavior is an expression of dominance with spatial consequences. By excluding individuals from an area, territory owners not only demonstrate their superior competitive abilities for the resources contained within a defended area, but they influence the location of others within a population as well. Given this, the presence of others within a territory is not easily explained, since subordinate group members, by depleting territorial resources, must represent a cost to dominant individuals. To adequately understand group formation within territories, the factors that compensate

dominant individuals for the costs that subordinate group members represent must be identified.

Benefits of group living

For dominant striped parrotfish, this compensation clearly exists. Within territories, dominants enjoy reasonably high feeding rates in the presence of lower-ranking group members, and this rate dropped significantly when a subordinate was removed (Figs. 1 and 2). These decreases in feeding presumably reflect a drop in the food intake rate of dominant fish, since changes in food density within territories did not accompany removals (Tables 1 and 2).

Changes in the feeding behavior of dominant fish apparently stem from several different subordinate behaviors. Most obviously, subordinate participation in the defense of a territory allows dominant fish to spend more time feeding. When defending subordinates were removed, dominant individuals were induced to spend more time protecting their territory (Fig. 1). Traditionally, (indeed, almost by definition) the sharing of defense by territorial group members has been considered to be an integral component of group territorial systems (e.g., Brown 1969, 1982; Gaston 1978; Woolfenden and Fitzpatrick 1978; Craig 1979; Davies and Houston 1984) and, in at least one case, appears to be the primary reason that some individuals share their territories (Davies and Houston 1981). Thus, patterns of shared defense among striped parrotfish are consistent with those found in other group territorial systems.

The removals of non-defending fish demonstrate that defense sharing is not the only factor influencing the feeding rate of a dominant individual, however. As might be expected, the absence of these subordinates did not affect the time a dominant spent defending its territory. Instead, the removal caused dominant fish to spend less time feeding and more time swimming (Fig. 2).

These reduced feeding rates apparently reflect increased search times for food since dominant fish also took longer to discover introduced food patches following removals. Specifically, this implies that non-contributing subordinates are tolerated within striped parrotfish territories because they aid in the detection of good food patches (similar conditions may contribute to group formation in some bird flocks, e.g., Baker 1978; Baker et al. 1981; Barnard and Sibly 1981; Rohwer and Ewald 1981; Czikeli 1983; Barnard 1984; Giraldeau 1984). Reductions in a dominant's feeding time could also be due to increased vigilance for preda-

tors (as a result of reduced group size; e.g., Pulliam 1976; Bertram 1978; Caraco 1979; Pulliam and Caraco 1984), although the manner in which striped parrotfish detect predators suggests this is less likely (Clifton 1989). In either event, both food-finding and predator vigilance have, to date, been considered simply as two of a suite of possible factors which might, secondarily, contribute to the evolution of territory sharing behavior (e.g., Gaston 1978; Brown 1982). The results presented here suggest that one, or perhaps both, may contribute substantially to the benefits accrued by dominants and, thus, be a significant reason why certain individuals are tolerated within striped parrotfish territories.

Costs of group living

Any benefits accruing to dominant group members must be judged in relation to the costs of living together. As mentioned earlier, because subordinate group members consume some of the defended resources within a territory, they must represent something of a cost to dominant individuals. This cost may be reduced, however, if dominant behaviors effectively lower the harvest rate by subordinate group members (Pulliam 1976; Brown 1982). Additionally, studies of other territorial groups have shown that these costs may be further reduced if subordinates tend to feed in areas that are unattractive or unavailable to dominant individuals (e.g., Macdonald 1983, 1984; von Schantz 1984; Carr and Macdonald 1986). Of course, this must have some limits, with resource depletion eventually limiting the food intake of dominants as groups become larger. Otherwise, territorial defense against smaller fish would seem unnecessary, and we might expect immense groups to form.

Both of these factors apparently limit the food intake of subordinate striped parrotfish and thus reduce the cost they represent to dominant fish. Not only do dominance interactions within parrotfish territories lower the overall rate at which subordinates feed (Fig. 4), they must also, to some extent, diminish a subordinate's access to areas of relatively high algal abundance (dominant fish invariably excluded subordinates from high quality food patches once the patch was discovered). Thus, when subordinates do feed, it is probably often within patches already depleted by dominant group members. This may explain why algal densities did not change following subordinate removals. Resource levels within a striped parrotfish territory are probably more a function of where, when, and how often different group members

feed, rather than simply a function of the number of individuals present within the territory.

Analogous conditions have been found among territorial groups of social Canids (e.g., Macdonald 1983; Carr and Macdonald 1986). Within these groups, distinct patterns of resource use by dominant and subordinate individuals reduce the degree to which low-ranking group members deplete territorial resources. For territorial striped parrotfish, however, spatial and temporal variation in both resource abundance and usage is probably regulated more by the foraging behavior of dominants than by intrinsic environmental features (as in other group territorial systems, e.g., Bradbury and Vehrencamp 1976; Macdonald 1983; Carr and Macdonald 1986). Thus, for these fish, the ability of a dominant to influence the behavior of another group member plays an important role in reducing the costs that an additional individual represents.

In conclusion, it is the apparent interplay of increased benefits and reduced costs to dominant individuals that has led to the development of group territorial behavior among striped parrotfish. The results reported here demonstrate that, in the presence of subordinates, dominant fish defend their territory less often, spend more time feeding, and have priority of access to many of the resources contained within the defended area. In contrast, group living apparently reduces the food intake of subordinate striped parrotfish, yet they remain within groups. This is presumably due, as in other group territorial systems, to the costs associated with life outside of territories and, perhaps, to the potential future benefits gained after ascending to a position of higher rank within a group. Ultimately, it is the ability of one individual to dominate over another that contributes to the economic defensibility of striped parrotfish group territories, and this has led to the formation of stable territorial groups in the absence of kin-selection and without the elaborate patterns of cooperative behavior that characterize so many other group territorial systems. This result should encourage further studies on the role that individual differences play in the evolutionary development and maintenance of group territorial behavior.

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References

- Aitchison J (1982) The statistical analysis of compositional data. *JR Statist Soc B* 2:139–177
- Baker MC (1978) Flocking and feeding in the great tit, *Parus major*: an important consideration. *Am Nat* 112:779–781
- Baker MC, Belcher CS, Deutsch LC, Sherman GL, Thompson DB (1981) Foraging success in junco flocks and the effects of social hierarchy. *Anim Behav* 29:137–142
- Barlow GW (1975) On the sociobiology of four Puerto Rican Parrotfishes (Scaridae). *Marine Biology* 33:281–293
- Barnard CJ (1984) The evolution of food-scrounging strategies within and between species. In: CJ Barnard (ed) *Producers and scroungers: strategies of exploitatic and parasitism*. Chapman and Hall, New York, pp 95–126
- Barnard CJ, Sibly RM (1981) Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim Behav* 29:543–550
- Bertram BCR (1978) Living in groups: predators and prey. In: JR Krebs, NB Davies (eds) *Behavioural Ecology*. Blackwell Scientific Publications, Oxford, pp 64–96
- Bradbury JW, Vehrencamp SL (1976) Social organization and foraging in Emballonurid bats. II. A model for the determination of group size. *Behav Ecol Sociobiol* 2:383–4
- Brown JL (1964) The evolution of diversity in avian territorial systems. *Wilson Bull* 76:160–169
- Brown JL (1969) Territorial behaviour and population regulation in birds: a review and re-evaluation. *Wilson Bull* 81:293–329
- Brown JL (1974) Alternate routes to sociality in jays with a theory for the evolution of altruism and communal breeding. *Am Zool* 14:63–80
- Brown JL (1978) Avian communal breeding systems. *Annu Rev Ecol Syst* 9:123–156
- Brown JL (1982) Optimal group size in territorial animals. *J Theor Biol* 95:793–810
- Buckman NS, Ogden JC (1973) Territorial behavior of the striped parrotfish, *Scarus croicensis* Block (Scaridae). *Ecology* 54:1377–1382
- Caraco T (1979) Time budgeting and group size: a theory. *Ecology* 60:611–617
- Carpenter FL, MacMillen FE (1976) Threshold model of feeding territoriality and test with a Hawaiian honey creeper. *Science* 194:639–642
- Carpenter FL, Patton DC, Hixon MA (1983) Weight gain and adjustment of feeding territory size in migrant hummingbirds. *Proc Natl Acad Sci USA* 80:7259–7263
- Carr GM, Macdonald DW (1986) The sociality of solitary foragers: a model based on resource dispersion. *Anim Behav* 34:1540–1549
- Clifton KE (1989) Territory sharing by the striped parrotfish, *Scarus iserti*: patterns of resource abundance, group size, and behaviour. *Anim Behav* 37:90–103
- Craig JL (1979) Habitat variation in the social organization of a communal gallinule, the pukeko, *Porphyrio porphyrio melanotus*. *Behav Ecol Sociobiol* 5:331–358
- Czikeli H (1983) Agonistic interactions within a winter flock of slate coloured juncos (*Junco hyemalis*): evidence for dominants' strategy. *Z Tierpsychol* 61:61–66
- Davies NB, Houston AI (1981) Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. *J Anim Ecol* 50:157–180
- Davies NB, Houston AI (1984) Territory economics. In: JR Krebs, NB Davies (eds) *Behavioural Ecology* 2nd edn. Blackwell Scientific Publications, Oxford, pp 148–169
- Emlen ST (1982) The evolution of helping. I. An ecological constraints model. *Am Nat* 119:29–39
- Emlen ST (1984) Cooperative breeding in birds and mammals. In: JR Krebs, NB Davies (eds) *Behavioural Ecology* 2nd edn. Blackwell Scientific Publications, Oxford, pp 305–309
- Gaston AJ (1978) The evolution of group territorial behavior and cooperative breeding. *Am Nat* 112:1091–1100
- Gill FB, Wolf LL (1975) Economics of feeding territoriality in the golden-winged sunbird. *Ecology* 5:333–345
- Giraldeau LA (1984) Group foraging: the skill pool effect and frequency-dependent learning. *Am Nat* 124:72–79
- Hart DD (1987) Feeding territoriality in aquatic insects: cost benefit models and experimental tests. *Am Zool* 27:371–386
- Koenig WD, Pitelka FA (1981) Ecological factors and kin selection in the evolution of cooperative breeding in birds. In: RD Alexander, DW Tinkle (eds) *Natural selection and social behavior: recent research and new theory*. Chiron Press, New York, pp 261–280
- Koford RR, Bowen BS, Vehrencamp SL (1986) Habitat saturation in groove-billed anis (*Crotophaga sulcirostris*). *Am Nat* 127:317–337
- Lindström E (1986) Territory inheritance and the evolution of group-living in carnivores. *Anim Behav* 34:1825–1835
- Macdonald DW (1983) The ecology of carnivore social behaviour. *Nature* 301:379–384
- Macdonald DW (1984) A reply to von Schantz. *Nature* 307:390
- Mares MA, Lacher TE Jr (1987) Social spacing in small mammals: Patterns of individual variation. *Am Zool* 2:293–306
- Myers JP, Conners PG, Pitelka FA (1979) Territory size in wintering sanderlings: the effects of prey abundance and intruder density. *Auk* 99:551–561
- Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish, *Scarus croicensis* Block (Scaridae). *Ecology* 54:589–96
- Pulliam HR (1976) On the advantages of flocking. *J Theor Biol* 38:419–422
- Pulliam HR, Caraco T (1984) Living in groups: is there an optimal group size? In: JR Krebs, NB Davies (eds) *Behavioral Ecology* 2nd edn. Blackwell Scientific Publications, Oxford, pp 122–147
- Pyke GH (1979) The economics of territory size and time budget in the golden-winged sunbird. *Am Nat* 114:131–145
- Randall JE (1983) *Caribbean reef fishes*. 2nd edn. T.F.H. Publications, Hong Kong
- Randall JE, Randall HA (1963) The spawning and early development of the atlantic parrotfish, *Sparisoma rubripinne*, with notes on other Scarid and Labrid fishes. *Zoologica*, 48:49–60
- Robertson DR, Sweatman HPA, Fletcher EA, Clelland MG (1976) Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology* 57:1208–1220
- Robertson DR, Warner RR (1978) Sexual patterns in the labroid fishes of the western Caribbean. II. The parrotfishes (Scaridae). *Smithson Contrib Zool* 255:1–26
- Rowher S, Ewald PW (1981) The cost of dominance and advantage of subordination in a badge signalling system. *Evolution* 35:441–454
- Schoener TW (1971) Theory of feeding strategies, 2. *Rev Ecol Syst* 2:369–404

- Temeles EJ (1987) The relative importance of prey availability and intruder pressure in feeding territory size regulation by harriers, *Circus cyaneus*. *Oecologia* 74:286–297
- Vehrencamp SL (1977) Relative fecundity and parental effort in communally nesting anis (*Crotophaga sulcirostris*). *Science* 197:403–405
- Vehrencamp SL (1978) The adaptive significance of communal nesting in groove-billed anis (*Crotophaga sulcirostris*). *Behav Ecol Sociobiol* 4:1–33
- von Schantz T (1984) Carnivore social behaviour: does it need patches? *Nature* 307:389
- Warner RR, Downs IF (1977) Comparative life histories: Growth vs. reproduction in normal males and sex-changing hermaphrodites in the striped parrotfish, *Scarus croicensis*. *Proc 3rd Int Symp on Coral Reefs. (Biology)* 1:275–282
- Woolfenden GE, Fitzpatrick JW (1978) The inheritance of territory in group-breeding birds. *Bio Science* 28:104–108
- Woolfenden GE, Fitzpatrick JW (1984) *The Florida Scrub Jay*. Princeton University Press, Princeton
- Ydenberg RC, Krebs JR (1987) The trade-off between territorial defense and foraging in the Great Tit (*Parus major*). *Am Zool* 27:337–346