Territory sharing by the Caribbean striped parrotfish, *Scarus iserti*: patterns of resource abundance, group size and behaviour

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Abstract. Along the Caribbean coast of Panama, female groups of the striped parrotfish, *Scarus iserti*, co-defend a common area against neighbouring territorial and roving non-territorial conspecifics. Unlike many other group territorial organisms, the individuals within these groups are unrelated to one another and express no parental care. This paper describes the patterns of resource abundance, territory size, group membership and activity associated with the territory sharing behaviour of these fish. These data are applied to a set of hypotheses which may explain the evolution of parrotfish group territorial behaviour. The results suggest that groups form within territories because socially dominant individuals can exploit food resources more efficiently when others are present. This is due, at least in part, to the sharing of territorial defence, which allows individuals more time to feed. Other benefits of group-living, such as improved vigilance for predators or more efficient searching for food, may also enhance a territorial individual's food intake, while dominance interactions limit the consumption of resources by subordinates. The potential interaction of these factors in determining individual payoffs invites further study on the specific costs and benefits associated with life in these non-kin territorial groups.

Territorial behaviour ostensibly evolves when the costs of excluding others from resources are outweighed by the benefits an individual accrues from enhanced access to those resources (Brown 1964). Since territoriality, by definition, involves the exclusion of others from an area, the selective forces that lead to territory formation are often perceived to conflict directly with the advantages of group-living. Group territorial behaviour, the sharing of a single territory by several individuals, might therefore seem somewhat paradoxical. All else being equal, an increase in the number of residents competing for the limited resources within a territory should reduce per caput resource levels, making territory sharing less advantageous than exclusive territory use.

There are, nevertheless, many examples of groups of individuals mutually defending a common area, particularly among cooperatively breeding organisms (reviewed by Emlen 1984). In these cases, the benefits derived from certain aspects of territorial group-living apparently offset the costs of resource depletion that additional individuals represent. Two factors in particular appear to promote the formation of territorial groups: (1) environmental constraints (e.g. a shortage of suitable habitat or mates) that lower an individual's likelihood of establishing a successful territory (e.g. Brown 1969; Emlen 1982; Woolfenden & Fitz-

patrick 1984; Koford et al. 1986); and (2) benefits gained as a consequence of living in a group. These benefits may be realized directly, via interactions among group members (e.g. the shared care of young), as well as indirectly, as a result of kin selection (e.g. Brown 1974; Gaston 1978; Vehrencamp 1978; Koenig & Pitelka 1981).

The specific costs and benefits of territorial behaviour have been examined in detail for a number of territorial systems in which a single individual defends an exclusive area (e.g. Gill & Wolf 1975; Carpenter & MacMillen 1976; Myers et al. 1979; Pyke 1979; Carpenter et al. 1983; McFarland 1986; Hart 1987; Mares & Lacher 1987; Temeles 1987; Ydenberg & Krebs 1987). In contrast, the economics of group territorial living remain relatively unexplored. While the question of precisely how an individual may benefit from defending a group territory has been treated theoretically on numerous occasions (Brown 1974, 1982; Gaston 1978; Macdonald 1983; Davies & Houston 1984; von Schantz 1984; Carr & Macdonald 1986; Lindstrom 1986), the empirical data corroborating these ideas are difficult to obtain (although see Davies & Houston 1981 for groups of two). Complex kin relationships, a lack of alternative social strategies for comparative purposes, and elaborate patterns of shared parental care tend to obscure exactly how the maintenance of a group

territory, by itself, ultimately influences an individual's fitness.

This paper examines the territorial behaviour of a Caribbean coral reef fish, the striped parrotfish, *Scarus iserti*. These fish express group territorial behaviour in the absence of kin selection and shared parental care. The data presented here show how patterns of territory size, group size and resource distribution influence per caput food availability inside of territories. They also demonstrate how the behaviour of other group members (e.g. territorial defence or dominance interactions) may affect an individual's food intake rate. The results are applied to a set of hypotheses that may account for the evolutionary development of group territoriality in the absence of kin selection and the shared care of offspring.

Background

The striped parrotfish is an abundant herbivorous coral reef fish. Usually found in relatively calm, shallow water, they spend much of their time grazing on filamentous microalgae and benthic diatoms that accumulate on dead coral rubble and sand. Like many other parrotfish and wrasses, striped parrotfish change sex and have two distinct colour phases; smaller males and females display a striped initial phase, while larger individuals are in the more colourful, terminal phase. These larger individuals are always male (Randall 1983).

Striped parrotfish are generally found in one of three distinct social contexts: as residents of territories; as members of large roving schools; or as part of smaller, non-territorial, stationary groups (Ogden & Buckman 1973). Territorial females defend algal resources (Buckman & Ogden 1973), while territorial males (almost always of terminal phase) defend mating territories that usually encompass several female territories. Individuals in the roving schools and stationary groups are of varied size and sex (Ogden & Buckman 1973; Warner & Downs 1977) and appear to compete directly with territorial individuals for the protected food inside territories (Robertson et al. 1976). Striped parrotfish spawn daily throughout the year (Robertson & Warner 1978), and mate either in pairs (a terminal phase male and a female) or in groups (many males and a single female).

Along the coast of Panama, several female striped parrotfish are often found within a single feeding territory (Buckman & Ogden 1973; Warner

& Downs 1977). These fish have an extended planktonic larval stage, eliminating the possibility that closely related individuals are consistently found in the same area. Their eggs are spawned directly into the water column, with no subsequent parental care.

There are a variety of evolutionary reasons why striped parrotfish might be found sharing a single feeding territory. Below, I consider the most plausible of these as a set of general hypotheses. These hypotheses are discussed from the point of view of the largest resident female within each group, since these individuals can presumably control group size and composition, if control is possible.

Hypotheses

Null hypothesis

Additional individuals may be tolerated within a territory if they represent insignificant costs and benefits to dominant territorial striped parrotfish. Theoretically, territory owners should only defend an area against competitors that threaten to reduce protected resources (Low 1971; Myrberg & Thresher 1974; Ebersole 1977; Macdonald 1983; Carr & Macdonald 1986). If certain conspecifics have minimal dietary overlap with larger female parrotfish (e.g. they eat different foods or they only consume food inaccessible to, or unwanted by, dominant fish), then dominant fish should not waste time excluding these individuals from an area. In this case, 'grouping' within a territory is simply a consequence of distinct, yet spatially overlapping foraging patterns, with no additional selection for group formation. Thus, microhabitat differences in foraging behaviour should exist between group members. If these dietary differences are size related, then large individuals should not defend against smaller fish and fish of similar size should not be found living in the same territory.

Net cost hypothesis

The presence of additional individuals may represent a net cost to dominant territorial females if the overall costs of admitting a specific individual are lower than the costs of excluding it. Groups within territories may still persist, however, as long as the continued exclusion of other individuals ultimately generates a greater payoff than does non-territorial behaviour. This could apply to striped parrotfish territoriality in several ways.

(1) Certain individuals may be persistent in their

attempts to invade a territory. Thus, for a given rate of invasion, the willingness of a territory holder to tolerate an individual should be directly related to the potential costs of resource depletion the intruder represents. Smaller individuals, with presumably lower food intake rates, would therefore be more likely to be accepted within a territory than larger invaders. Shared defence of the territory is not a necessary prediction of this hypothesis.

(2) Smaller individuals, perhaps by virtue of their size, may be able to avoid eviction from territories (e.g. by using refuges within a territory). Thus, large individuals of similar size should not be found residing in the same territory. As above, smaller individuals would not necessarily be expected to participate in defence of the area, particularly against large fish. As smaller fish grow larger they should eventually be driven from the territory.

(3) Females may be forced into closer proximity because of the direct interference of larger, socially dominant males (e.g. Peterson 1968; Clutton-Brock et al. 1982). By impeding the defensive attempts of territorial females and coercing females into groups, male striped parrotfish may cause an increase in female densities and subsequently enjoy higher reproductive success. Thus, males should directly interfere with the territorial defence by females against conspecifics. Additionally, they should intervene during aggressive interactions between group members. Large females should drive off smaller fish in the absence of males.

Net benefit hypothesis

Large territorial females may receive a net benefit from group formation within territories. This may occur for several reasons.

(1) The absolute amount of resources available per individual may be greater within group territories, particularly if groups are better than solitary individuals at defending certain areas (up to some limit, Brown 1969, 1982). Thus, all group members should participate in the defence of a territory. When resources are distributed homogeneously between territories, larger groups should defend disproportionately larger areas, resulting in a positive geometric correlation between group size and territory size. Alternatively, if resources are distributed heterogeneously between territories, then larger groups should defend areas of higher resource quality. In either case, there should be more per caput resources available to group-living

individuals. This hypothesis does not require any further advantages of group formation.

(2) Group territorial organisms may use available resources more effectively than solitary individuals because of activities such as shared defence or vigilance for predators (Gaston 1978; Brown 1982; Davies & Houston 1984). Dominant individuals, in particular, may improve their access to resources (e.g. by usurping food patches discovered by subordinates, Baker 1978; Barnard & Sibly 1981; Rohwer & Ewald 1981; or by inducing subordinates to perform a disporportionate share of the territorial defence, Gaston 1978; Brown 1982). This hypothesis could work in concert with 1, above, if behaviours such as shared defence also lead to a per caput increase in resource availability, or could be the sole reason that territorial groups form. In this case, fish within groups should spend more time feeding than solitary territorial individuals (especially dominant individuals). Defence sharing is expected. If dominant individuals use other group members as food-finders then an increase in their feeding rate is expected following the displacement of a subordinate. A relationship between available resources and group size is not necessary.

METHODS

Territory Structure

Populations of territorial striped parrotfish were monitored on six patch reefs and one large fringing reef among the San Blas islands off the Caribbean coast of Panama. The study was conducted over a 3-year period (dates of study: June–December 1983, March–September 1984, April–August 1985, and March–May 1986). I captured many of the fish within each study area by herding them into a wall net measuring 1.5×8 m (mesh size 0.6×0.6 cm). These fish were measured, sexed and individually tagged using subcutaneous injections of a vital dye (Alcian Blue). All fish were released back onto their territories within 40 min of their capture.

To facilitate repeated, long-term observations of specific sites, I marked the boundaries of 167 territories on the seven reefs. Three of the patch reefs were small enough (reef area less than 500 m²) to allow every territory on the reef to be monitored. On the three larger patch reefs and the fringing reef, areas containing territorial parrotfish were arbitrarily chosen and all territories within that area

were subsequently mapped. I estimated territory boundaries using two criteria: (1) the location of escalated defensive encounters characterized by jaw fighting (Buckman & Ogden 1973), and (2) the locations at which fish pursued by a diver would attempt to flee back towards the interior of the territory. The second method was much simpler, and provided estimates of boundary location that were always within 0·4 m of the estimates generated using the former method ($\bar{X} \pm 1\text{SE} = 0·18 \pm 0·07$ m, $N = 37$). I calculated the area of 79 of these territories by measuring their perimeters and mapping them on finely gridded graph paper (grid size scaled to 0·1 m).

The size and composition of territorial groups of parrotfish were determined from censuses of all fish within known territory boundaries. I noted the presence of any tagged individuals and also recorded the estimated size of each fish inside the territory. All 19 territories on one patch reef were checked daily for 30 days and then observed again 1 month later to assess the short-term stability of these groups. I also conducted occasional censuses of tagged individuals over a period of months to establish longer-term patterns of residency.

I measured food levels by sampling algal growth on artificial reef substrates. On four of the study reefs, sets of 15 unglazed ceramic tiles ($2·6 \times 2·6$ cm) were placed at arbitrarily chosen sites either inside territories or in areas outside of territories where non-territorial striped parrotfish were seen feeding. Each set of tiles was initially arranged in a three by five manner, covering a 101·4-cm^2 area. All tiles were left unmanipulated for at least 45 days. In most cases, a set of tiles was placed at only one site within a territory. In two territories on one reef, however, sets of 15 tiles were placed at four and five sites, respectively, so that potential differences in algal abundance among sites within a territory could be assessed. To determine the amount of algae at a particular site at any one time, I collected a randomly chosen tile from the set of tiles associated with that site. All algae were scraped from the tile's upper surface and preserved in 10% buffered formalin. Because the samples contained a proportion of sand and other inorganic matter, I obtained an ash-free dry weight for each sample.

To establish that this sampling method provided a reasonable estimate of the actual amount of algae present in an area, I also collected algae from actual reef substrate. Inside of one territory, sets of three tiles were placed adjacent to six naturally occurring

areas of coral rubble. After 45 days, all tiles within the territory were collected. Within 5 min, algae were also scraped from three $2·6 \times 2·6$-cm areas on pieces of coral rubble lying next to each set of tiles. Ash-free dry weights were obtained for all samples in both sets.

Behaviour

I used an underwater tape-recorder to obtain time budgets of striped parrotfish behaviour. To develop an average profile of a particular fish's behaviour, focal individuals were monitored during 5-min bouts, on at least 5 days, at the same time each day. During a 5-min bout, the time the focal animal spent actively feeding, defending, swimming between activities, and displacing or being displaced by another group member was recorded. In addition, I monitored the number of bites taken while feeding. For all interactions with other individuals, the identity (other group member, neighbour, intruder, etc.) and size of the other fish were noted. Five of the territories used for the time-budget analyses were gridded on a 0·5 m scale, and locations of all events were also noted. On one reef I also collected time-budget data for five non-territorial females that foraged as members of a moderately large foraging school (more than 150 individuals). All of the non-territorial fish observed were of similar size to subordinate territorial fish, ranging in length from 57 to 74 mm.

RESULTS

Territory Structure

Striped parrotfish territories were found at depths ranging from 1 to 30 m, although they were most common at depths less than 10 m. On the patch reefs, territories were located along the reef base, lying juxtaposed to one another in the fringe of sand and dead coral rubble surrounding the reef. There were very few undefended areas on these reefs. In contrast, territories on the fringing reef were clustered side by side in shallow water areas of rubble and sand where live coral cover was sparse. On this reef, large undefended expanses of apparently similar substrate were adjacent to those areas occupied by territorial parrotfish. Non-territorial parrotfish roved through these areas regularly.

Territories ranged in size from 2·80 to 19·00 m^2 ($\bar{X} = 9·24 \pm 0·36$ m^2, $N = 79$; all means ± 1 SE unless
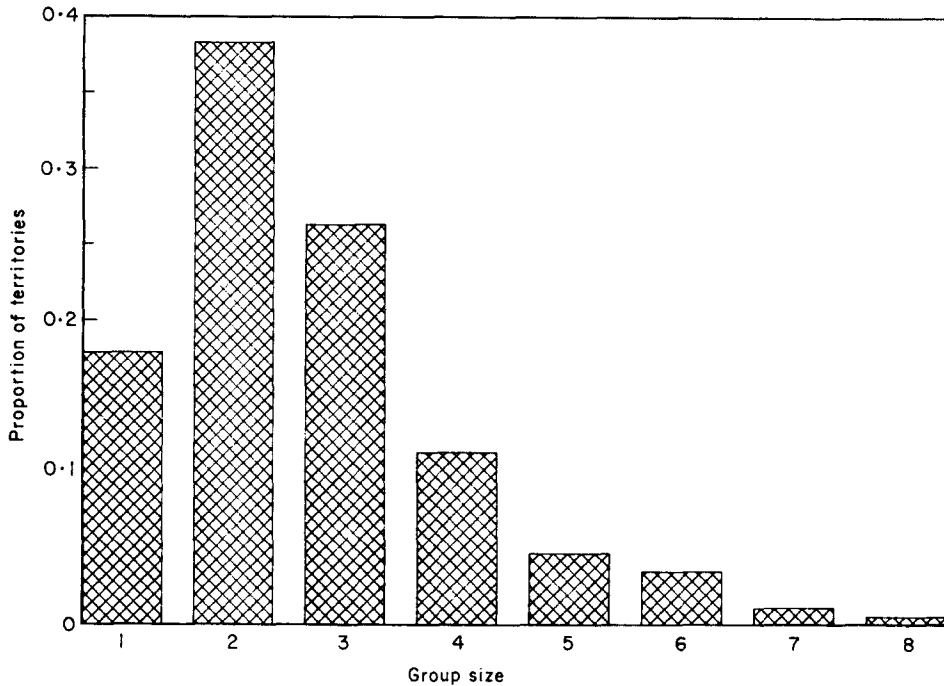
Figure 1. Frequency distribution of territorial group sizes ($N = 167$, $\bar{X} \pm \text{SE} = 2 \cdot 71 + 0 \cdot 11$).

otherwise noted) and group size varied from one to eight individuals (Fig. 1). There was no relationship between group size and territory area (Fig. 2). Territorial individuals were either adult females or smaller, immature fish of undetermined sex, ranging in size from 30·7 to 123·0 mm (all fish sizes are standard length). I found no consistent size distribution within groups, save that all groups possessed at least one fish larger than 75 mm. Often, two, and sometimes three individuals of similar size (less than 2 mm difference in length) occupied the same territory.

Overall, these territorial groups were quite stable, with the same individuals occupying the same territories day after day (only twice during the entire tenure of the study did an individual naturally change residency from one territory to another). Tagged individuals were often found within their original territories for more than a year. On six occasions, a small fish (less than 45 mm) was recruited into an existing group as a low-ranking subordinate, becoming a permanent resident (mean recruits per territory per day $= 4 \cdot 8 \times 10^{-3} \pm 3 \cdot 1 \times 10^{-3}$, $N = 1243$ territory-days). Losses from the group were of two basic types: the departure of large females (greater than 85 mm)

that left the group only after initiating sex change, and apparently random disappearances of individuals of all sizes (over a 2-month period four individuals disappeared from 19 territories on one reef). These disappearances were presumably due to mortality since missing fish were never found elsewhere on a reef and striped parrotfish tend not to emigrate to other reefs (Ogden & Buckman 1973). Observations and recaptures of tagged fish revealed that territorial individuals grew approximately 25 mm per year and thus, barring mortality, should remain within a territory for about 2 years. Territory boundaries did not appear to change during the course of my study, even with shifts in group size and composition.

The mean amount of algae found on tiles within territories ($4 \cdot 6 \times 10^{-3} \pm 1 \cdot 0 \times 10^{-4}$ mg/cm^2, $N = 343$; all weights from ash-free dry samples) was significantly greater than the mean amount found on tiles outside of territories ($3 \cdot 2 \times 10^{-3} \pm 1 \cdot 0 \times 10^{-4}$ mg/cm^2, $N = 76$, $T = 4 \cdot 751$, $P < 0 \cdot 001$). Group size did not have a significant effect upon the amount of algae found within a territory (ANOVA: $F_{3,199} = 1 \cdot 08$, $P = 0 \cdot 36$), however, there was a significant negative relationship between the mean amount of algae available per caput and the
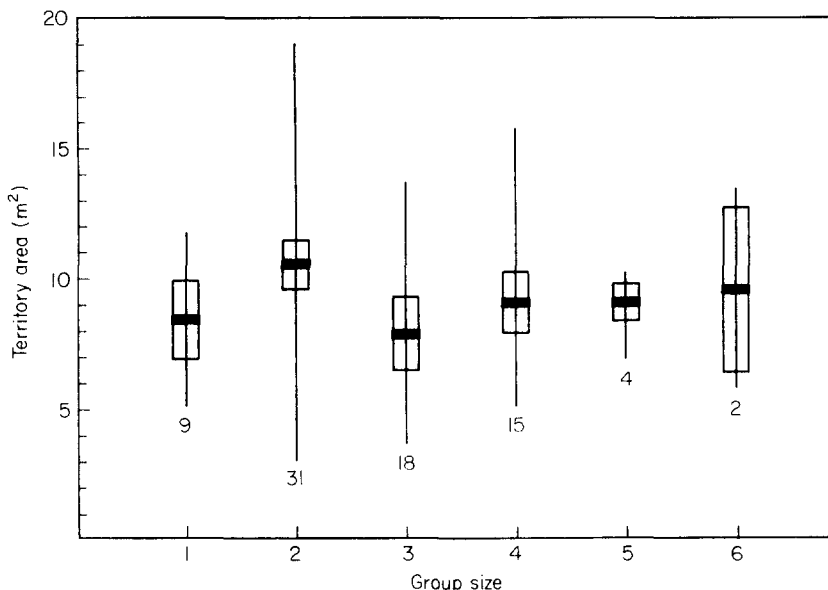
Figure 2. Mean territory area as a function of group size ($R^2 = 0.06$, $P = 0.521$). Boxes are ± 1 SE, vertical lines are ranges.

size of the group (Fig. 3). Sites within territories were roughly equivalent to one another, with no significant effect of either site or time upon the amount of algae collected from two territories (nested two-way ANOVA: $F_{7,56} = 1.01$, $P = 0.44$, and $F_{7,56} = 0.69$, $P = 0.68$, respectively). Thus the density measures obtained from a particular site within a territory provided a reasonable estimate of the overall food density inside a territory, and hence, the level of resources available to a territorial individual.

Although the samples used to measure the amount of algae present were obtained from artificial substrate, they apparently matched the quantity and, at least in some respects, the quality of algae growing upon natural substrate. There were no significant differences in either the amount of algae collected, or the percentage of inorganic material present, when algal samples collected from ceramic tiles and from real substrate were compared (ANOVAs: $F_{1,29} = 0.19$, $P = 0.67$ and $F_{1,29} = 0.13$, $P = 0.73$, respectively). Striped parrotfish appeared to treat tiles as they did any other algal-covered substrate, and were regularly observed grazing algae from tiles.

Behaviour

Site use by group members overlapped exten-

sively, with each group member moving freely throughout all parts of the defended area. On average, 81·9% of the available substrate inside a territory was used for grazing (from detailed maps and time-budget surveys of five territories, SE = 1·5). The only areas within a territory where parrotfish were not observed foraging were either outcrops of live coral or large patches of macroalgae (surfaces on which microalgae tended not to accumulate). Several species of damselfish (genus *Stegastes*) sometimes maintained small, exclusive territories within those areas defended by striped parrotfish. Since striped parrotfish were never observed inside these damselfish territories, I did not consider these areas to be part of a parrotfish's territory.

I found no evidence of behavioural partitioning of the territory among group members; all residents of a territory were seen foraging in the same areas, although not necessarily at the same time. Group members also defended a common territory perimeter. In 14 of 167 territories, very large females (all larger than 93 mm) occupied two adjacent territories, both of which were maintained separately by one or more smaller individuals.

All group members contributed to the defence of an area, although the burden of defence was generally not shared equally. The contribution of a particular fish to the overall defence of a territory
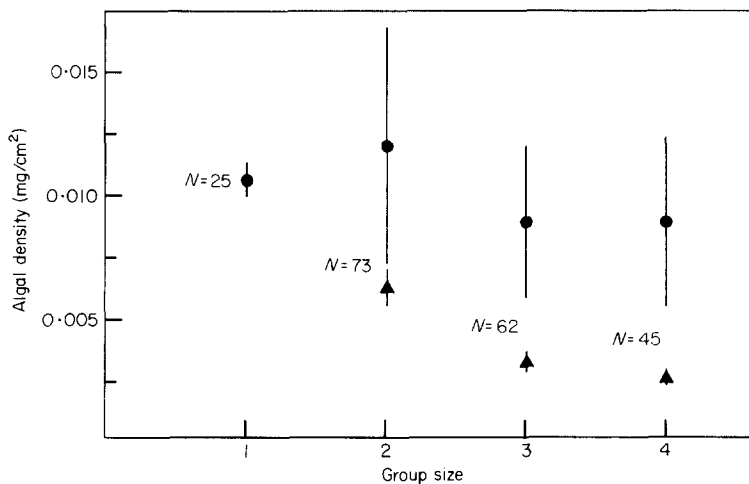
Figure 3. Mean algal density found within territories as a function of group size. Circles are overall means, triangles are per caput means (for log transformed per caput ash-free dry weights; $R^2 = 0.60$, $P < 0.001$). Vertical lines are ± 1 SE.
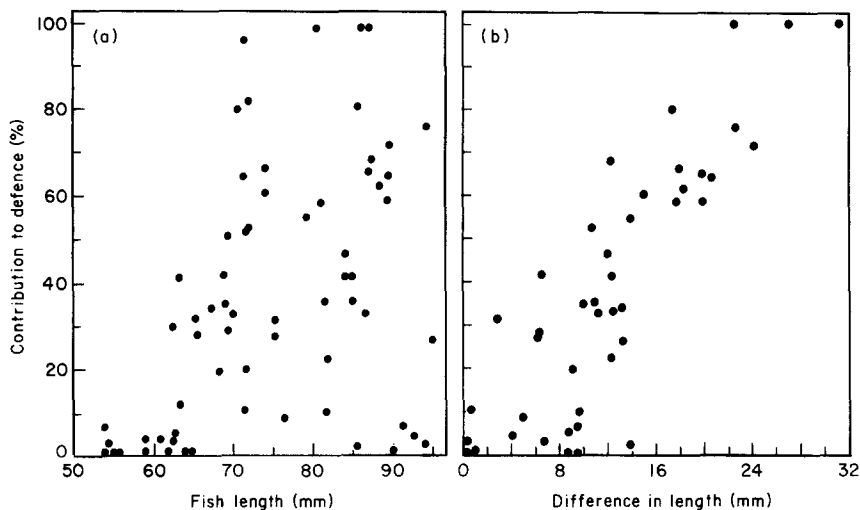
Figure 4. An individual's contribution to the defence of a territory as a function of (a) the length of the fish (regression on arcsine transformed proportions; $R^2 = 0.31$, $P = 0.27$), and (b) the difference in size between an individual and the next smallest group member (regression on arcsine transformed proportions; $R^2 = 0.71$, $P < 0.001$).

was related to both an individual's size and the size of other group members. Regardless of group composition, small individuals (less than 65 mm) rarely participated in territorial defence, although overall, absolute size was not related significantly to an individual's contribution to defence (Fig. 4a). Relative size was a better predictor of how much an individual contributed to the defence of a territory. The greater the difference in size between two individuals, the greater the contribution to overall

defence by the larger of the two (Fig. 4b). Rates of defence also appeared to be related to the size of an intruder, with smaller territorial fish seldom defending against individuals of much larger size (in every case in which this occurred, however, they were successful at excluding these large intruders) and larger fish tending not to defend against small intruders (Fig. 5). On average, individuals living in groups spent significantly less time defending their territories (3.73 ± 0.52 s defending/5 min, $N = 83$)
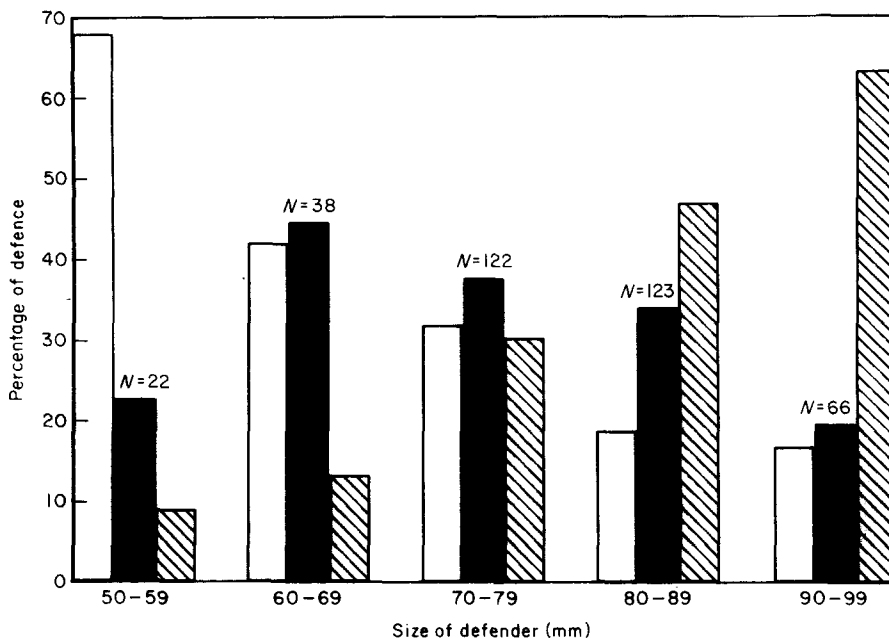
Figure 5. Percentage of defence performed against intruders of different size as a function of defender size. Intruder size is represented as follows: open bars: less than 65 mm; closed bars: 65–80 mm; hatched bars: greater than 80 mm. All sizes are standard length.

than did solitary territorial individuals ($15 \cdot 21 \pm 2 \cdot 37$ s defending/5 min, $N = 19$, $T = 7 \cdot 39$, $P < 0 \cdot 001$). Among territories with two or more residents, however, there was no effect of group size upon the per caput rate of defence (ANOVA: $F_{2,79} = 0 \cdot 84$, $P = 0 \cdot 44$).

Within a 5-min period, territorial fish devoted time to foraging, defence and interactions with other group members. Territorial individuals generally spent over half their time foraging, either feeding in sporadic bouts of varied length or swimming between feeding sites. Within bouts of feeding (defined as a series of bites in which each bite was within 2 s of another), the mean rate of biting was relatively constant for all fish ($1 \cdot 59 \pm 0 \cdot 01$ bites per s, $N = 402$), with no effect of fish size on bite rate (ANOVA: $F_{1,400} = 0 \cdot 02$, $P = 0 \cdot 90$). Diurnal patterns of parrotfish behaviour, particularly foraging rates, were influenced by a number of environmental factors such as water clarity, cloud cover, wave action and time of day, but all group members appeared to be similarly affected by these factors.

Although they took up relatively little time, aggressive interactions between group members were common. Social status within a group was

associated with size, and most dominance interactions appeared to be food-related; larger fish would supplant smaller ones during bouts of feeding. Immediately following a displacement, a dominant individual's mean feeding bout length was significantly higher ($13 \cdot 88 \pm 1 \cdot 37$ s, $N = 48$) than its mean feeding bout length otherwise ($6 \cdot 26 \pm 0 \cdot 37$ s, $N = 195$, $T = 5 \cdot 37$, $P < 0 \cdot 001$). The number of subordinates present within a group also appeared to influence a dominant individual's feeding behaviour since the amount of time a dominant individual spent feeding was positively correlated with the size of a group (Fig. 6a). Conversely, the rates at which subordinate individuals fed were quite variable and showed no overall relationship to group size (Fig. 6b).

Social status within a territory also influenced feeding rate relative to the rate at which non-territorial parrotfish fed. On one of the smaller reefs, where no foraging school was present and non-defended substrate was absent, there was an overall effect of class (dominant, subordinate, or non-territorial individual) upon the mean proportion of time spent feeding (ANOVA: $F_{2,141} = 42 \cdot 34$, $P < 0 \cdot 001$). A test of means revealed that the mean proportion of time spent feeding by non-territorial
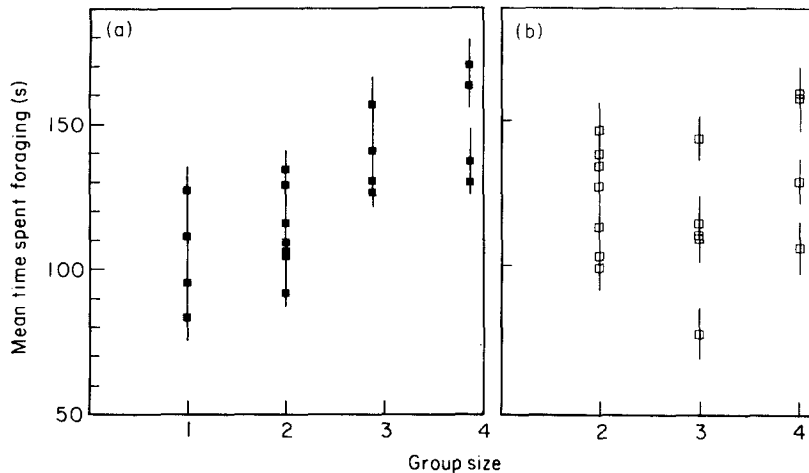
Figure 6. Mean time spent foraging (per 5-min observation period) as a function of group size for (a) dominant territorial individuals ($R^2 = 0.35$, $P < 0.005$) and (b) subordinate territorial individuals ($R^2 = 0.03$, $P = 0.13$). Vertical lines are ± 1 SE.

individuals (which were relatively uncommon) was significantly lower (17.6 ± 4.5 s feeding/5 min) than the mean proportion of time spent feeding by dominant territorial individuals (97.35 ± 3.9 s feeding/5 min, $F_{1,141} = 81.63$, $P < 0.001$), as well as subordinate territorial individuals (99.1 ± 5.4 s feeding/5 min, $F_{1,141} = 75.49$, $P < 0.001$).

In contrast, on one of the larger reefs (where a foraging school was present) there was no overall effect of class upon feeding rate (ANOVA: $F_{2,33} = 2.03$, $P = 0.15$). However, a test of means revealed that the mean proportion of time spent feeding by subordinate territorial fish (116.6 ± 9.1 s of feeding/5 min) was significantly less than the mean proportion of time spent feeding by five similarly sized members of a non-territorial foraging school (141.3 ± 6.4 s feeding/5 min, $F_{1,33} = 4.05$, $P = 0.05$). A test of means also revealed no significant difference between the mean proportion of time spent feeding by these non-territorial individuals and the mean proportion of time spent feeding by dominant territorial fish (129.2 ± 13.2 s feeding/5 min, $F_{1,33} = 0.82$, $P = 0.37$).

DISCUSSION

Lacking kinship and parental care, striped parrotfish might seem an unlikely candidate to express group territorial behaviour. However, their shared defence of common boundaries, their overlapping foraging areas and their stable groups certainly qualify them as a group territorial species. Group formation within these territories has apparently evolved because dominant individuals can spend more time feeding when others are present within a territory (Fig. 6a), suggesting that group-living enhances their ability to exploit territorial resources. Increases in feeding rate presumably reflect a net increase in the rate of food intake since, overall, fish had similar bite rates while feeding and the amounts of algae present within territories held by groups of different size were not significantly different (Fig. 3). These gains in the ability to harvest territorial resources apparently outweigh the costs of resource depletion caused by additional group members (Fig. 3).

None of the other hypotheses that might account for the expression of group territorial behaviour by striped parrotfish was supported by my observations. Large and small fish within a territory foraged in the same areas and dominance interactions between individuals of different sizes were food-related; these findings are counter to the idea that group members do not compete for the same resources (null hypothesis). Similarly, there was no evidence that territorial groups form because smaller fish are more persistent intruders or can evade eviction by larger individuals (net cost hypotheses 1 and 2); dominant individuals showed

no propensity to tolerate only small fish, small fish were not driven from territories as they grew larger, and, commonly, several larger fish of similar size would reside within the same territory (this observation also detracts from the null hypothesis).

I sometimes did observe males interfering with female territorial defence (suggesting that perhaps female density within a territory increased as a result; net cost hypothesis 3). It was, however, a relatively uncommon event, generally restricted to the approximately 2-h mating period each day when females, aggregating at spawning sites near a territory boundary, might express defensive behaviour. These encounters apparently had nothing to do with group membership, occurring almost exclusively among neighbours rather than fellow group members or non-territorial intruders. Finally, I found nothing to suggest that groups defended certain areas such that more food was available per group member (net benefit hypothesis 1). There was no relationship between group size and territory area (Fig. 2), and a negative correlation between group size and the average amount of food available to each individual within a territory (Fig. 3). Opposite to the prediction of this hypothesis, per caput levels of available food declined with an increase in group size.

Payoffs to Dominant Individuals

Defence sharing

Several authors have proposed that the sharing of territorial defence can be a major benefit associated with group territoriality (Brown 1969, 1982; Gaston 1978; Davies & Houston 1981, 1984). Certainly, defence sharing can account for some of the increases in foraging time of dominant group territorial parrotfish (Fig. 6a). These individuals often continued to forage while another group member chased off an intruder, and, on average, fish in groups spent less time in defence than did their solitary counterparts.

Defence sharing has been shown to compensate for group-related reductions in territorial resources in at least one other instance of territory sharing (Davies & Houston 1981), and has been implicated in others (e.g. Caro & Collins 1986). Is this then the sole reason that territorial groups of striped parrotfish form? Given the extremely low defence rate of small fish (Fig. 4b), probably not. Instead, it seems

likely that other benefits of group-living are also inducing dominant striped parrotfish to accept others within a territory.

Other group-related benefits

For example, group-living may reduce the amount of time individuals spend searching for predators, allowing them more time to feed (Pulliam 1973). While little quantitative data are available either supporting or detracting from this idea (it was never clear whether a swimming parrotfish was actively searching for food or for predators), there is some qualitative evidence to suggest that predator detection has not been an important evolutionary component of parrotfish group formation.

When a potential predator approaches a section of coral reef, almost invariably all of the small fish in the area, regardless of species, dive to cover. If indeed striped parrotfish are cueing on the behaviours of others to aid in the detection of predators, it seems likely that dominant individuals use other species of fish (that are generally closer in proximity, much more numerous, and not competing for territorial resources) at least as much as they would conspecific group members. Thus, although some benefits may be gained from the detection of predators by fellow group members, it would appear that the role this benefit has ultimately played in the formation of these territorial groups of parrotfish has been of a secondary nature.

Studies of other organisms have either suggested or demonstrated that high-ranking individuals can exploit the ability of others to find food (i.e. by usurping food patches discovered by subordinates, e.g. Baker 1978; Baker et al. 1981; Barnard & Sibly 1981; Rohwer & Ewald 1981; Czikeli 1983; Barnard 1984; Giraldeau 1984). This may also apply to striped parrotfish. Recall that dominance interactions were food-related and that dominant individuals had longer bouts of feeding immediately after displacing another individual. By supplanting others from areas of relatively high algal abundance, dominant individuals may reduce their overall search time for food and increase their opportunities to forage in richer patches of algae. Some degree of spatial heterogeneity in algal distribution presumably exists within striped parrotfish territories (probably at a finer scale than my sampling methods could detect, and due, at least in part, to the variable lengths of time since particular areas have been grazed). Given the

manner in which dominance behaviour is expressed within territorial groups, it seems plausible that dominant individuals are exploiting this variation in patch quality by displacing subordinates from regions of relatively high algal abundance.

There is also a possibility that dominant individuals induce subordinates to perform a disproportionate share of the overall defence of a territory (perhaps by the threat of eviction). Whenever two group members were matched closely in size, invariably the larger, dominant individual contributed little towards defence of the territory (Fig. 4b). It is interesting to note that subordinates of similar size to dominant fish probably represent the greatest potential cost in terms of resource depletion within a territory, and thus seem likely candidates for domination. It remains to be seen, however, whether or not the observed relationship between patterns of defence and relative fish size is a direct consequence of the dominant behaviour of the larger fish.

Costs

The consumption of common resources by subordinate fish must represent something of a cost to dominant individuals. However, dominant behaviours that reduce the amount of time a subordinate individual spends feeding should, all else being equal, diminish the degree to which lower-ranking individuals consume those resources. The ability to dominate other group members may therefore be reducing the overall cost that lower-ranking individuals represent to larger fish. This cost will be ameliorated even further if subordinates tend to feed in areas where the standing crop of algae is relatively low (as mentioned above, some temporal heterogeneity in the distribution of food is presumably present whenever renewing food resources such as algae are being intermittently grazed). It seems likely that the degree of resource depletion occurring within parrotfish territories is primarily a function of both the feeding rates of individuals (that are being influenced by other group members) and the location and timing of feeding events, rather than strictly by the number of individuals present within a group. This could account for the lack of a significant relationship between increasing group size and the amount of algae present within a territory (Fig. 3). In any case, if dominance interactions within a group do act to reduce the rate at which subordinate group members deplete terri-

torial resources, then the ability to dominate others may ultimately be a very important factor contributing to the formation of stable territorial groups, especially in systems where group members are unrelated.

Payoffs to Subordinate Group Members

Thus far, I have specifically focused upon the payoffs a dominant striped parrotfish receives from the presence of others within a territory, primarily because these individuals presumably have the ability to evict any other group member, controlling group size and composition in the process. It is also important, however, to consider why subordinate individuals might accept low social rank within a territory rather than defending their own territory or opting for some other social strategy. This is particularly true, given that in some cases, subordinates inside of territories fed at lower rates than did non-territorial fish of similar size.

Several factors may induce parrotfish of low rank to remain within a territorial group, even if the benefits they receive from group living are diminished because of dominance interactions. Most obviously, subordinate individuals may be found within groups simply because the potential rewards from life elsewhere are very low and group territorial living is, ultimately, the best available strategy. For many other group territorial species this appears to have been an important factor contributing to the evolutionary development of group territorial behaviour (e.g. Emlen 1982, 1984; Woolfenden & Fitzpatrick 1984; Koford et al. 1986). For striped parrotfish, this condition might apply to those fish living on small reefs, where almost all of the suitable substrate is held by territorial individuals (either parrotfish or damselfish) and population sizes are not great enough to support a successful foraging school of non-territorial striped parrotfish. Non-territorial parrotfish on these small reefs fed at extremely low rates, suggesting that there is a significant cost to living outside of a territory.

In contrast, non-territorial fish on larger reefs fed at higher rates than did subordinate territorial fish. This suggests that low-ranking fish might increase their food intake if they left the group. While it may be the case that non-territorial life under these conditions is relatively more costly (e.g. because non-territorial fish may have to swim at faster rates, spend more time foraging in areas of

reduced algal abundance, or be at higher risk of mortality), it is also possible that subordinate parrotfish are found within territorial groups for other reasons.

For example, even if habitat appropriate for territory formation is available (as appears to be the case on larger reefs), subordinate individuals may be unable to maintain exclusive territories simply because dominant striped parrotfish (who benefit from the presence of subordinates within a territory) may move into territories held only by smaller fish. This would effectively reduce the relative cost to subordinates of living inside a territorial group. It could also explain why very large striped parrotfish sometimes occupy two adjacent territories that are both maintained by smaller fish. Robertson (1984) described an analogous situation in which two Caribbean species of damselfish defend overlapping territories, and the larger, more dominant of the two species, benefits from the defensive behaviour of the other.

Regardless of the relative short-term payoffs obtained from group-living, subordinates may remain within a group simply because of the long-term benefits derived from the eventual accession to a position of higher status within the group (e.g. West Eberhard 1975; Woolfenden & Fitzpatrick 1984). This may be particularly applicable to striped parrotfish since, unlike many other group-forming species, the departure of a dominant individual from a group is a relatively predictable event, related more to size and sex-change than to mortality. Indeed, it could be argued that the more a subordinate individual improves the food intake rate of a higher-ranking individual (e.g. by defending the territory more or by functioning as a food-finder) the sooner the dominant individual will leave the group. This could increase the likelihood that the subordinate will someday become the highest-ranking group member. In any case, if long-term benefits are an important factor, then rank, and the associated probability of eventual accession to top-ranking dominance status, may significantly influence the degree to which a subordinate contributes to the overall maintenance of a territory (Gaston 1978), and this may be the case within striped parrotfish territories. Large subordinates were the individuals that generally contributed the most to territorial defence and these fish have a relatively high probability of becoming the top-ranking member of a group.

In conclusion, it appears that group territorial behaviour among striped parrotfish has evolved primarily because of two aspects of their group-living: the sharing of territorial defence and the ability of larger group members to dominate others. These factors not only allow dominant territory residents to spend more time feeding, they also presumably reduce the extent to which additional group members deplete the food resources within a territory. Subordinates presumably remain within these groups both because of the costs of non-territorial life and the potential for future rewards within a territory.

Traditionally, other aspects of group territorial life, such as kin selection and cooperative brood care have been invoked to explain why several individuals might defend a common area. The territorial behaviour of striped parrotfish suggests that these are not necessary conditions for the development of group territoriality. An increase in benefits as a consequence of group-living, combined with factors that diminish the costs of resource depletion that additional group members represent, appear to be sufficient to promote the formation of stable, non-kin, territorial groups.

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