Subordinate group members act as food-finders within striped parrotfish territories

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Abstract: Female striped parrotfish *Scarus iserti* (Block) defend small feeding territories from conspecifics. Within these, large territorial individuals typically tolerate several smaller fish, perhaps because subordinate group members hasten the dominant's detection of good food patches. To test this idea, naturally occurring groups of striped parrotfish were presented with small patches of high quality food in a series of controlled experiments. Overall, time to patch discovery was inversely related to group size as was the time to discovery by the dominant fish. In addition, dominant fish had priority of access to patches once they were discovered. Thus, in the presence of subordinates, dominant striped parrotfish found and exploited rich food patches faster. This advantage apparently offsets the costs of resource depletion that subordinate group members represent and has ultimately contributed to both the formation and persistence of these stable territorial groups.

INTRODUCTION

The caribbean striped parrotfish *Scarus iserti* (Block) faces the challenge of finding and exploiting ephemeral patches of microalgae. Females of the species meet this challenge, in part, by defending territories against conspecific intruders (Buckman & Ogden, 1973). Typically, large females tolerate several smaller fish inside their territory (Clifton, 1989). While the tolerance of certain subordinates stems from their help in territory defense (Clifton, 1990), this explanation cannot account for the presence of nondefending fish within the territory.

In flocking birds, the tolerance of subordinates is often linked to the search for food, because dominant birds may increase their foraging efficiency by usurping food discovered by others (e.g., Baker, 1978; Rowher & Ewald, 1981; Czikeli, 1983). Dominance interactions among striped parrotfish mimic this pattern, and large territorial parrotfish might also use subordinates as "food-finders".

I tested this hypothesis, in situ, by presenting naturally occurring groups of striped parrotfish with food patches of known quality. Groups of varied size were used and time

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to patch discovery was measured for each group member. I predicted an inverse relationship between group size and time to discovery if dominant individuals use subordinates to find food.

METHODS

A small grazing herbivore, the striped parrotfish abounds throughout the Caribbean (Randall, 1983). Several studies have described their sex-changing life history and relatedly complex social organization (Ogden & Buckman, 1973; Barlow, 1975; Robertson & Warner, 1976; Warner & Downs, 1977). Foraging individuals are found either in foraging schools (Ogden & Buckman, 1973; Robertson et al., 1976) or in territories (Buckman & Ogden, 1973). The experiments described here involved territorial individuals and were performed among the San Blas islands of Panama from March to May 1986.

A recent study of striped parrotfish territorial behavior (Clifton, 1989) found up to eight unrelated females residing within a territory, although groups of two and three were most common. Territory size was unrelated to both group size and the amount of food present within territories. Dominance, defined as the ability to displace others during bouts of feeding, was strictly size related; and stable linear dominance hierarchies persisted within territories (Clifton, 1989).

The diet of these fish consists primarily of fast growing epiphitic microalgae and benthic diatoms (Randall & Randall, 1963; Randall, 1983). These occur on a variety of inorganic substrata. As ephemeral resources, their abundance at any one spot within a territory varies depending, in part, upon the time since an area was last grazed.

To verify this patchiness, five sets of 15 unglazed ceramic tiles (2.6 × 2.6 cm; each set arranged in a 3 × 5 manner) were arbitrarily placed within two territories (group size of two in both). These were left unmanipulated for 45 days (resulting algal mats on tiles do not differ in either quantity or quality from naturally occurring algal mats in the same area; Clifton, 1989). Three tiles from each set were then collected daily for 5 days. Collections were made between 1300 and 1400 and all algae scraped from the upper surface. Samples were preserved in 10% buffered formalin and later analysed for ash-free dry weight.

To determine if dominant individuals use other group members to help find good food areas, "patches" growing on tiles were introduced into territories. Two treatments of tiles were used, generating two types of algal patches: "rich" patches, protected from grazing by 0.6-cm mesh hardware cloth for 3 days prior to the experiment; and "control" patches, unprotected from grazing and located immediately adjacent to the covered tiles. In six cases before an experiment, three tiles from each treatment were collected and treated as above.

An experiment began with the placement of either a "rich" or "control" tile at a randomly chosen location within a territory. Time until one of the territorial residents

took its first bite of algae was then recorded, as was the identity of the group member (individuals were lightly tagged with unique patterns of subcutaneously injected Alcian blue at least 45 days before the experiments). Subsequent discovery times and identities also were recorded. Observations ended 10 min after patch introduction, regardless of outcome. For all groups (four each of group sizes one and two; two each of group sizes three and four), four presentations each of a "rich" and a "control" patch were performed in random order. All presentations were done between 1200 and 1400. For a particular group, only one tile presentation was performed per day, and time of presentation was randomized among groups. Tiles were collected immediately after the observation period and algae were scraped and preserved as above.

RESULTS

The daily collection of tiles verified a patchy food distribution within territories. Over the 5-day period, algal abundances at a specific site fluctuated unpredictably from one day to the next (Fig. 1). Although, through time, a site did not differ from itself or other
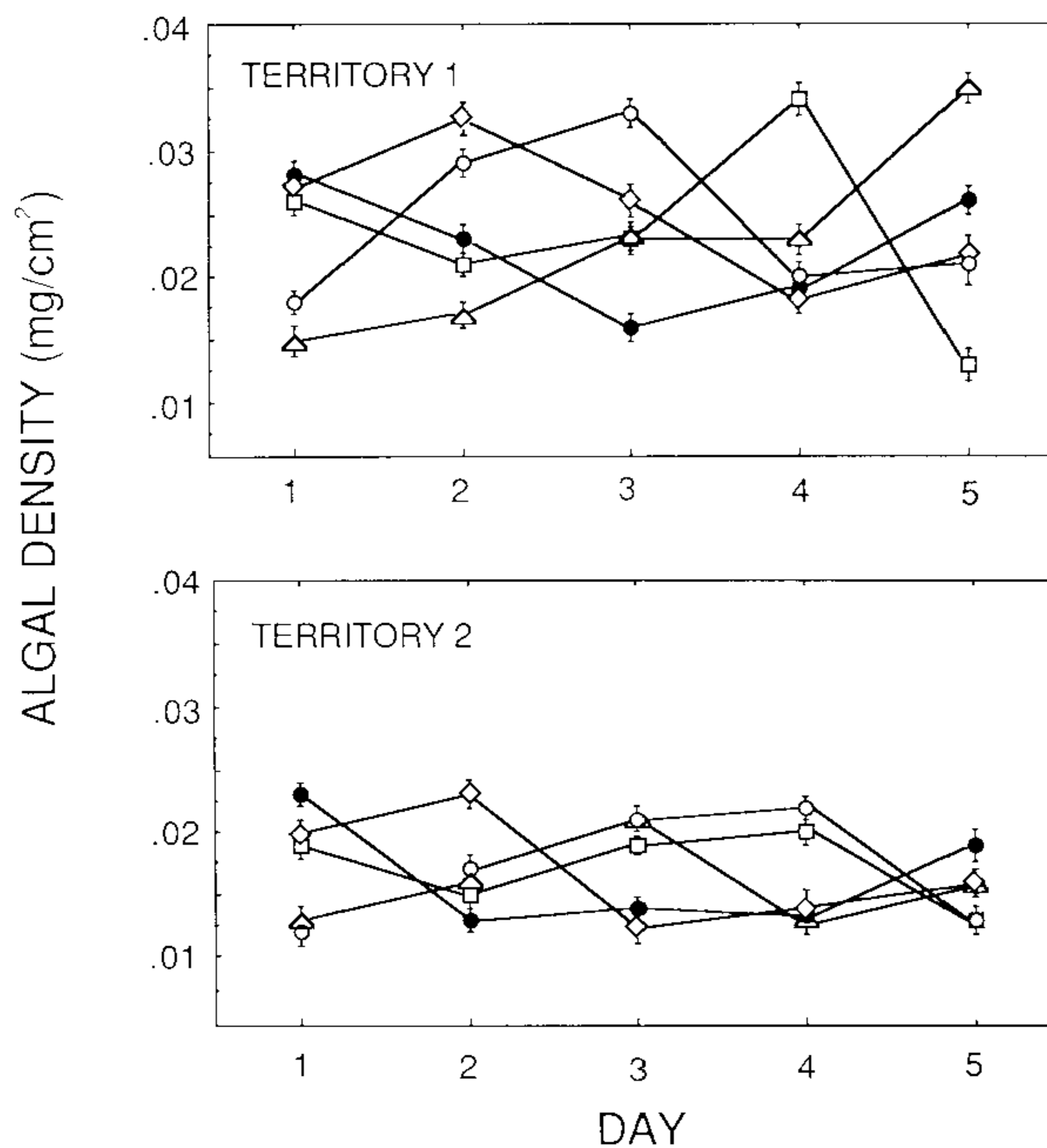

Fig. 1. Changes in feeding patch quality (mean algal density $\pm$ 1 SE) inside two striped parrotfish territories (group size of two in both). Symbols represent five different sites within each territory, sampled on 5 consecutive days.

sites within the territory (respectively; repeated measures ANOVA; Territory 1: $F_{4,74} = 1.68$; $P = 0.23$ and $F_{4,74} = 1.28$; $P = 0.29$; Territory 2: $F_{4,74} = 1.02$; $P = 0.44$

and $F_{4,74} = 1.83$; $P = 0.14$), the significant interaction between site and time (Territory 1: $F_{4,74} = 23.92$; $P < 0.001$; Territory 2: $F_{4,74} = 10.22$; $P < 0.001$) reveals that at a given time, algal density differed from site to site within a territory, and that sites differed from themselves from one day to the next.

Covered tiles were indeed "richer", with approximately twice the mean density of algae growing on them ($2.3 \times 10^{-2} \pm 1.1 \times 10^{-3}$ mg·cm^{-2}; all weights ash-free and all $\bar{x}$ values ± 1 SE) than uncovered tiles ($1.2 \times 10^{-2} \pm 1.0 \times 10^{-3}$ mg·cm^{-2}; ANOVA; $F_{1,35} = 54.14$; $P < 0.001$). When these "rich" patches were discovered, fish immediately began feeding in a rapid series of bites. Subordinate discoverers were invariably displaced by a larger group member, often after foraging for only a few seconds. The displacer then fed uninterruptedly, unless a still larger group member displaced it.

TABLE I

Mean number of seconds to discovery of rich and control patches by striped parrotfish overall (first discovered) and for dominant group members (dominant discovered). All $\bar{x}$ values are ± 1 SE.

Territorial group size	Rich patches			Control patches		
	First discovered	Dominant discovered	ND[a]	First discovered	Dominant discovered	ND
1	315.5 ± 233.0	–	2	172.0 ± 85.0	–	2
1	291.0 ± 21.0	–	2	508.0 ± 73.0	–	2
1	364.0 ± 57.1	–	1	226.5 ± 34.5	–	2
1	308.0 ± 195.0	–	2	319.0 ± 132.0	–	2
2	229.0 ± 98.1	249.0 ± 100.0	0	501.5 ± 50.5	576.0 ± 24.0	2
2	187.0 ± 74.6	192.3 ± 80.1	1	286.0 ± 20.5	326.3 ± 34.1	1
2	266.0 ± 105.0	272.3 ± 110.3	0	138.7 ± 61.2	241.0 ± 163.5	1
2	150.3 ± 56.8	185.0 ± 78.9	2	163.5 ± 151.5	ND	1
3	118.3 ± 33.0	140.0 ± 34.4	0	379.0 ± 142.0	ND	2
3	124.3 ± 70.4	173.3 ± 52.9	1	435.3 ± 107.4	462.0 ± 120.4	1
4	37.0 ± 25.0	67.3 ± 19.9	1	384.0 ± 183.0	ND	1
4	57.7 ± 11.3	82.0 ± 20.2	1	156.0 ± 69.1	392.0 ± 86.1	2

[a] Patch not discovered within 10 min.

Throughout the experiments, dominant fish found good food patches faster in the presence of subordinates (Table I). Group size and the time to patch discovery by a territorial resident were negatively correlated, as were group size and time to discovery by the dominant individual (Fig. 2). This latter relationship suggests that subordinates were used as food-finders since the dominant initially discovered patches only 15% of the time. Group size and both initial discovery and discovery by a dominant were unrelated for "control" patches (regressions; $r^2 = 0.01$; $P = 0.99$ and $r^2 = 0.12$; $P = 0.07$, respectively).

The highest-ranking group member generally fed from a tile for several minutes before leaving and continuing to forage elsewhere. Algal density on the tile was visibly reduced at that time. Thus, dominant group members not only discovered good patches faster when subordinates were present (172.1 $\pm$ 25.5 s vs. 324.4 $\pm$ 55.6 s for solitary fish; ANOVA; $F_{1,34}$ = 7.94, P < 0.01), they consumed much of the algae growing there.
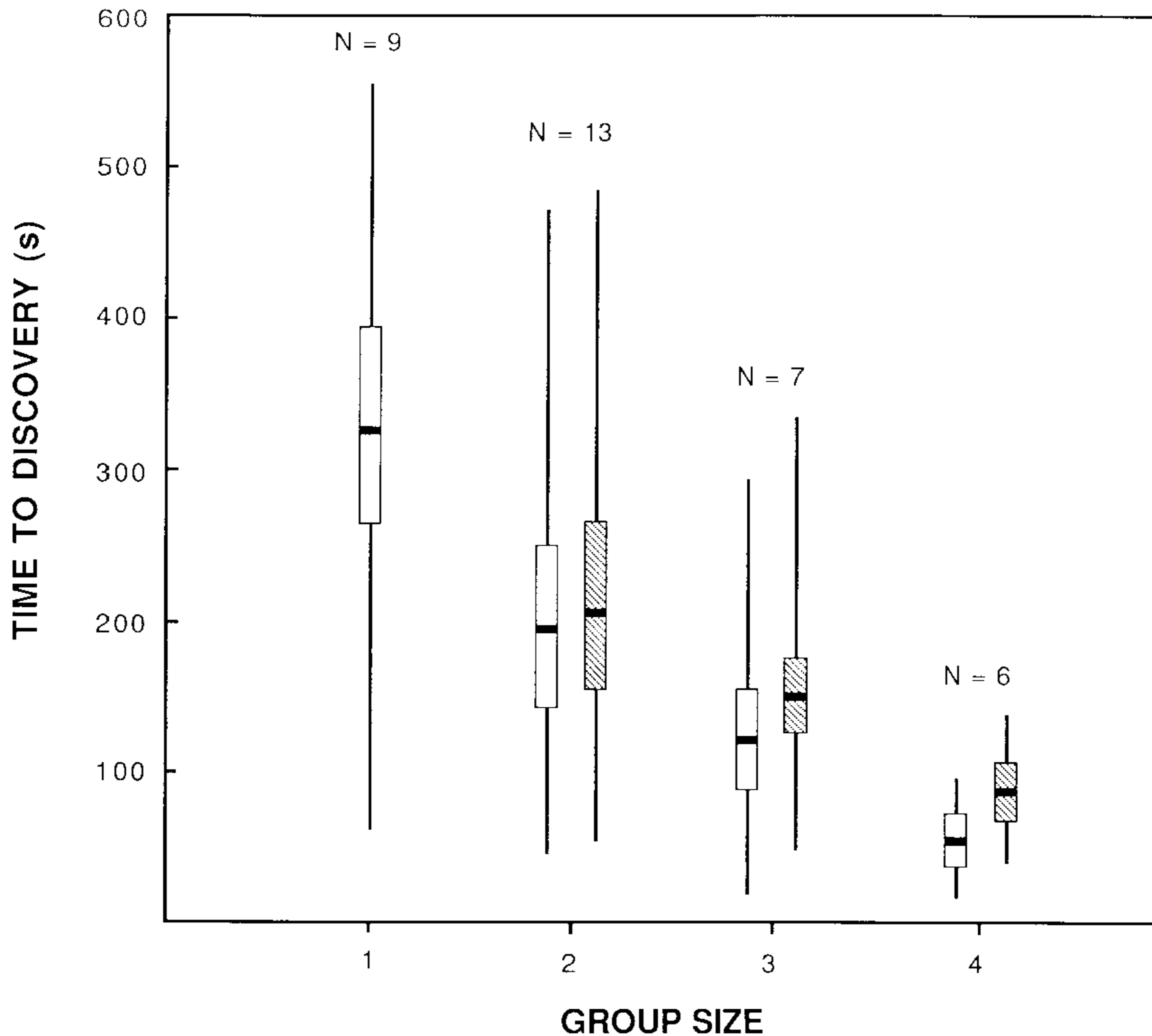

Fig. 2. $\bar{x}$, 95% confidence interval, and range of time to initial discovery of a "rich" patch as a function of group size by all territorial striped parrotfish (white confidence intervals; regression on log transformed data; r^2 = 0.38; P < 0.001) and by the dominant territorial resident (stippled confidence intervals; regression on log-transformed data; r^2 = 0.29; P < 0.001). Sample sizes reflect the number of trials in which the introduced patch was discovered.

Subordinate fish eventually fed on tiles, often extensively, but only after dominant group members had moved off. There was less algae on depleted "rich" tiles (collected after the experiments; 1.2 $\times$ 10^{-2} $\pm$ 0.7 $\times$ 10^{-3} mg $\cdot$ cm^{-2}) than on covered tiles collected at the beginning of the experiments (n = 66; t = 7.36; P < 0.001). Depleted tiles, instead, showed similar algal densities to control tiles (n = 66; t = 0.08; P = 0.94). Mean algal density on control tiles collected after the experiments (1.1 $\times$ 10^{-2} $\pm$ 0.7 $\times$ 10^{-3} mg $\cdot$ cm^{-2}) was not different from control tiles collected before (n = 66; t = 0.77; P = 0.44).

Discussion

Although stable groups persist under a variety of environmental conditions, specific regimes of predation pressure and resource distribution are generally perceived to be necessary precursors for group formation (e.g., Bertram, 1978; Pulliam & Caraco, 1984). As groups form, however, local resources will diminish, intensifying competition among group members. Competitive differences between individuals can then redistribute many advantages of group living towards specific group members. As a result, competitively inferior animals may then leave the group. In extreme cases, dominant individuals may even exclude others from an area by behaving territorially. Thus, the expression of dominance may often inhibit group formation.

In contrast, dominance by striped parrotfish apparently promotes group formation. Because subordinate fish improve a dominant's ability to find good food patches, they are tolerated within territories. This occurs even though large individuals could presumably maintain an exclusive area (as in many other territorial species; e.g., Gill & Wolf, 1975; Myers et al., 1979; Carpenter et al., 1983; Temeles, 1987).

Two conditions seem necessary for food-finding to be an important component of group formation. First and foremost lies the challenge of exploiting a relatively high quality but unpredictably patchy food resource. The daily collection of tiles from within territories verified this condition for striped parrotfish. Similar conditions have been found among bird flocks, where food-finding may also be important (e.g., Baker et al., 1981; Barnard, 1984). Second is the ability to easily dominate others. Escalated contests for food would quickly negate any foraging advantages gained from dominating. For striped parrotfish, size differences between group members obviously contribute to this condition, as does a stable group membership that allows for repeated interactions among individuals and the establishment of a dominance hierarchy. This contrasts sharply with birds, where individuals are often similarly sized and flock membership is quite labile. This may explain why status "badges" (Rowher & Ewald, 1981) have evolved in birds but not in parrotfish.

By using others as food-finders, a dominant can increase its own food intake while simultaneously reducing subordinate depletion of territorial resources. Constraints upon these benefits should contribute to patterns of group size and composition. For example, the positive correlation between food discovery and group size suggests that larger groups are generally more advantageous to dominant parrotfish. These fish cannot, however, exploit simultaneously discovered food patches and while a dominant forages in one patch, subordinates may feed in others. Thus, as group size increases, benefits accruing to a dominant from food-finding will eventually be negated by food depletion elsewhere. This will ultimately limit group size.

In addition, increasing discovery of good food patches should reduce variation in patch quality, since patch quality is, in part, a function of how long an area has gone ungrazed. The relative benefit gained from discovering "good" patches may be substantially reduced as group size increases, because patches will, on average, be more similar.

In combination, resource depletion and reduced patch variation may explain why groups of two and three striped parrotfish are most common (Clifton, 1989) even though dominants discovered food faster in groups of four.

Groups might also be small because subordinates refuse to live within large groups (e.g., Vehrencamp, 1983). With dominance interactions limiting their access to good food patches, low-ranking striped parrotfish must subsist upon food gleaned from previously exploited areas. The quality of these "leftovers" will presumably drop rapidly with increasing group size, and subordinates should abandon a group when food intake falls below what is available elsewhere. Carefully measuring the payoffs of nongroup living would resolve whether dominants or subordinates control group size.

In conclusion, food-finding behavior provides a good example of how dominance may contribute to stable group formation. Previously, this association had been linked primarily to bird flocking. The expression of dominance by territorial striped parrotfish establishes a broader role for the phenomenon and this should encourage further studies. It seems likely that additional examples of food-finding behavior will be found; particularly when food resources are both patchy and difficult to find, and when the ability to gain those resources differs from one individual to the next.

ACKNOWLEDGMENTS

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