Helping opportunities and space segregation in cooperatively breeding cichlids

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Studies of cooperative breeding have largely ignored the role of conflict among helpers and how it shapes group dynamics and helping behavior. In the present study, performing laboratory experiments with cooperatively breeding cichlids from Lake Tanganyika, we show that secondary group members (potential helpers) occupy home ranges within the group territory and may be aggressive to one another. Experimental removal of secondary group members allowed the individual next in rank to move closer to the removed individual's home range. In the field, dominant secondary group members stayed closer to the brood chamber than did subordinate group members of similar size, and proximity to the brood chamber was related to the length of time spent inside. We suggest that space segregation and competition among secondary group members is common in these cichlids, and may limit the opportunities to provide help. *Key words:* Cichlidae, competition, conflict, Lake Tanganyika, Neolamprologus, reproductive skew, territoriality. *[Behav Ecol 14:749–756 (2003)]*

The phenomenon of helping in cooperative breeding animals has stimulated a great deal of research (Brown, 1987; Cockburn, 1998; Emlen, 1991; Solomon and French, 1997; Stacey and Koenig, 1990; Woolfenden and Fitzpatrick, 1984). Nonetheless, despite the extensive research and numerous theoretical discussions, the question why group members help to raise young that are not their own remains open for debate (Brown, 1987; Cockburn, 1998; Connor and Curry, 1995; Stacey and Koenig, 1990; Wright, 1997; Zahavi, 1995). Furthermore, the factors that determine the amount of help provided by different individuals in a group are not entirely clear. Most studies to date have focused on helpers' contribution to the group's success and on the interactions between breeders and helpers. Only a handful of studies have focused on interactions among helpers and their effect on group dynamics and helping behavior (see Johnstone et al., 1999; Ligon and Ligon, 1978).

Recent theoretical studies have attempted to explore the variation in reproductive output between members of a cooperative group (Johnstone, 2000; Reeve, 2000). This framework is known as the reproductive skew theory. In most studies examining reproductive skew, it is assumed that dominant individuals in the group (i.e., the breeders) are responsible for the level of skew, either by giving concessions to subordinates (e.g., granting reproduction rights) or by simply failing to control subordinates' reproductive attempts (Clutton-Brock, 1998a,b; Emlen et al., 1998; Keller and Reeve, 1994; Reeve et al., 1998). This, in turn, may affect the level of help provided by the other group members, as a share in reproduction is expected to constitute an incentive for a member to help. However, competitive interactions among helpers may influence their access to food, shelter, helping, or reproductive opportunities, all of which may also affect the reproductive skew within the group.

Competitive interactions among helpers may also shed light on how helping behavior evolves. Carlisle and Zahavi (1986) argue that interference competition among helpers, in which dominant helpers suppress subordinates' helping attempts, cannot be explained by kin selection or group augmentation in which additional help should always be welcome. Interference competition may be predicted, however, if there is a direct benefit to the helper from performing helping behavior. Such direct benefits may be in the form of gaining social prestige (Zahavi, 1977, 1995), potential matings (Reyer, 1984), parental experience (Lawton and Guindon, 1981), or permission to stay in the breeders' territory (Balshine-Earn et al., 1998; Gaston, 1978; Mulder and Langmore, 1993; Taborsky, 1984). Despite the common notion that cooperative breeding has evolved mainly because of kin selected benefits (for a review, see Emlen, 1995), recent theoretical and empirical work suggests that the role of direct benefits in the evolution of cooperative breeding may deserve further attention (Balshine-Earn et al., 1998; Boland et al., 1997; Cockburn, 1998; Griffin and West, 2002; Heinsohn and Legge, 1999; Lotem et al., 1999; Nowak and Sigmund, 1998; Roberts, 1998). Although several studies have suggested that competition among helpers exists, the evidence for this is rare and anecdotal (Ligon and Ligon, 1978, 1983; Rasa, 1977) or is based on correlations (Carlisle and Zahavi, 1986) that more recent results for the same population have failed to support (Wright, 1997).

To examine whether or not potential helpers compete, we studied two cooperatively breeding cichlid species from Lake Tanganyika (*Neolamprologus brichardi* studied in the laboratory and *N. pulcher* studied in the field). These closely related species (or subspecies; see Grantner and Taborsky, 1998) are very similar in their social behavior and have been studied in both the field and the laboratory (Balshine-Earn and Lotem, 1998; Balshine-Earn et al., 1998, 2001; Taborsky, 1984, 1985; Taborsky and Limberger, 1981). Both species live in small colonies that consist of several groups. Each group consists of an alpha breeding pair and several smaller, subordinate individuals. These subordinate group members are commonly called helpers (see Taborsky and Limberger, 1981) as they fit the common definition of helpers in the cooperative breeding literature (see Brown, 1987; Cockburn, 1998). They often

perform the same behaviors as the breeders (broodcare, territory maintenance, and defense; Taborsky and Limberger, 1981) and reduce the breeders' workload by allowing breeders to feed more often, produce larger clutches (Balshine-Earn et al., 2001), and spawn more often (Taborsky, 1985). However, although these subordinate group members are tolerated by the breeders, they do not always help (see Results). Therefore, in this article we call these individuals secondary group members rather than using the conventional term helpers.

The aim of our study was to determine whether secondary group members compete, and whether such competition, if it exists, can affect their access to a shelter or to helping opportunities. We predict that if competition exists, it may be expressed in the form of aggression and space segregation among individuals. We also expect that if we experimentally remove the most dominant secondary group member, the individual next in rank would use the newly evacuated space and possibly also increase its helping behavior.

METHODS

Our study comprised both field and laboratory work. In the field, we conducted behavioral observations on pairs of size-matched secondary group members and also measured their home ranges. These observations were aimed to determine the possible behavioral and spatial effects of competition. In the laboratory, we conducted similar behavioral observations and spatial measurements, this time on all the secondary members in our experimental groups. We also conducted removal experiments in the laboratory, removing the most dominant secondary group member. The aim of this latter experiment was to test whether the next ranked secondary group member would respond in accordance with our competition hypothesis.

Laboratory observations and experiments

The experimental set-up
Eight groups of *N. brichardi* were each kept in separate aquaria at Tel-Aviv University (September 1997–January 1998). The aquaria (67.5-l aquariums: $90 \times 25 \times 30$ cm) were fitted with an external water filter, a heater, 2–3-mm gravel substrate, and two clay flowerpot halves. A 13 h/11 h light/dark regime and water temperature of 26–28°C were maintained. The fish were fed twice daily: dry food in the morning and frozen brine shrimp and chironomid larvae in the afternoon.

Each group was established by placing a set of five to eight randomly chosen young (25–40 mm in length) in an aquarium (hereafter, termed secondary group members). The number of young (five to eight) was determined by the availability of healthy individuals in the appropriate size. After at least 1 day of habituation, breeders were added (one adult male and female, unknown to the secondary group members). Such artificial groups have been previously shown to exhibit normal social behavior, including helping (see Taborsky, 1984, 1985). Before being placed in aquaria, all the fish were measured for standard length (SL) to 0.1 mm precision and for weight to 0.1 g precision. They were then individually marked by subcutaneous injection of nontoxic acrylic paint just below the dorsal fin. By using a number of different colors of paint and a number of unique spots on the body (below the dorsal fin), we generated a large number of individual marks that allowed us to recognize each fish in each group. The marking had no apparent effects on fish health or behavior. Because all individuals were marked by using the same method, it is also unlikely that some overlooked effects of the injection could bias our results in any systematic way.

We ranked all secondary group members based on their size (measured as SL, the length of the body from the tip of the snout to the caudal peduncle). Size predicts social rank in this species (von-Siemens, 1990), as well as in other fish species (see Booth, 1995). There were easily detectable size differences among secondary group members (range = 26.7–41.4 mm; mean difference between adjacent ranks = 1.5 mm).

Observations and experimental procedure
We observed the behavior and position of all the secondary group members in the eight groups from the day that the eggs were spawned (day 1) until the day that they hatched (day 3). Behavior recorded included overt aggression (e.g., ramming, biting, chasing, mouth fighting), submission (e.g., quivering, submissive postures) and dominance gestures (e.g., spreading fins, spreading opercula), brood chamber maintenance (e.g., digging, carrying) and direct brood care (e.g., micronipping eggs, carrying and guarding larvae; for complete ethograms, see Coeckelberghs, 1974; and Kalas, 1975). On days 1 and 2, each secondary group member in each family was visually observed, in random order, for 10 min. Although no focal observations were conducted on the breeding pairs, their interactions with each of the observed secondary group members were recorded. This data allowed us to assess the possible effect of breeders' behavior on space segregation among secondary group members (see Results). Position of the observed individual in the aquarium was recorded every 30 s by marking it on a two-dimensional scheme of the aquarium. After the observations on day 2, the largest secondary group member, assumed to be the dominant (see von-Siemens, 1990), was removed, and on day 3 we observed all the remaining secondary group members. All three observations started at the same time of day (1000 h).

The position data were digitized by using Techdig and Microsoft Excel and analyzed by using Wildtrak 1.22. By using these packages, we measured and analyzed two position parameters for each secondary group member: (1) the center of the area occupied by the individual during the observation (algebraic center: mean x, mean y), hereafter polygon center; and (2) the polygon area, calculated from polygons surrounding 95% of the position points marked during observations (excluding the most distant point from the center). Polygon centers were used to quantify the distance between two secondary group members, and polygon areas were used to quantify the overlap between polygons. For each pair of secondary group members, we measured the amount of overlap between their polygons by averaging the proportion of their overlapping areas (in percentages). Because measurements of distance and overlap among many pairs within the aquarium are unlikely to be statistically independent (and may be viewed as pseudo-replications), we used the means of these values in each aquarium as the independent data points for our statistical analysis (therefore $N = 8$). Most of the data deviated from the normal distribution, and therefore, nonparametric tests were used. Note that as a result, figures show box-plots in which the median and upper and lower quartiles of group means are presented. We calculated probability values for Wilcoxon signed-rank tests by using the t statistics (see Mundry and Fischer, 1998). All data were corrected for ties.

Field observations

Study site and selection of families
Field observations of *N. pulcher* were conducted from 16–31 March 1998 in Kasakalawe Bay, near Mpulungu, Zambia, in the southern part of Lake Tanganyika. All the data were collected by scuba diving to territories located at a depth of 6–11 m.

We selected 16 groups with two sexually mature (more than 35-mm SL) secondary group members of about the same size (range of SL = 36–54 mm; mean difference within a pair = 1.6 mm); these were the target individuals for the experiment. These target individuals were caught using hand nets and transparent PVC tubes, measured for SL, sexed, and marked by fin clipping and by injecting nontoxic acrylic paint subcutaneously or into scale pockets (see Balshine-Earn et al., 1998). We measured and marked the fish underwater, near their territories, processing each individual in 3–5 min. Dominance hierarchy among the target individuals was determined by behavioral interactions between the two, and if no dominant or submissive gestures were observed during 20 min of focal watches; the bigger fish was assumed to be the dominant (see von-Siemens, 1990).

Behavioral observations
Observations were conducted from 0700–0800 h. Target individuals were observed for 10 min each, during which their behavior and position were recorded manually on PVC slates. Behavior included territorial defense (against fish from other groups or against potential predators and species that compete for breeding substrate; see Balshine-Earn et al., 2001), overt aggression, and dominance and submission displays toward other group members (Coeckelberghs, 1974; Kalas, 1975). To quantify the amount of helping, we recorded the number of entries into the brood chamber and time spent inside, as it was not possible to observe brood care itself because eggs and young are tended underground inside an excavated brood chamber. Fish position was measured, once a minute, by estimating radius from the brood chamber and height off the ground. These estimates were combined to calculate an average distance from the brood chamber. Position data was recorded for 15 out of the 16 pairs of target individuals, and behavioral data was recorded for all pairs. We used the same software programs as in the laboratory experiment to analyze the field data (see above).

RESULTS

Space segregation among secondary group members

It was apparent from both our laboratory and field observations that different secondary group members occupied different home ranges within the group territory, and there was relatively little overlap between their home ranges. In the laboratory, secondary group members' use of space (represented by polygon area) was limited to an area much smaller than what would be expected if they moved freely throughout the entire aquarium (median polygon area = 149 cm^2 versus the area of the entire aquarium = 2250 cm^2; see example in Figure 1). Secondary group members were also located in the same position in the aquarium on consecutive days: polygon areas measured on consecutive days were of similar size (Wilcoxon signed-rank test, $T = 498$, $n = 49$, $p = .48$), and had a considerable amount of overlap between days (Figure 2a, right panel). Moreover, their algebraic centers (see Methods) were located nearly in the same location on days 1 and 2 (Figure 2b, right panel), and their x and y position coordinates in days 1 and 2 were highly correlated ($r_s = .90$, .82, respectively, $n = 49$, $p < .001$). In contrast to the high degree of overlap between the space used by each individual on day 1 versus day 2, the mean degree of overlap between any two particular secondary group members' polygons was small (Wilcoxon signed-rank test, $T = 0$, $n = 8$, $p = .01$) (Figure 2a, see also Figure 1). Similarly, the mean distance between polygon centers in day 1 versus day 2 for secondary group members was smaller than the mean distance between
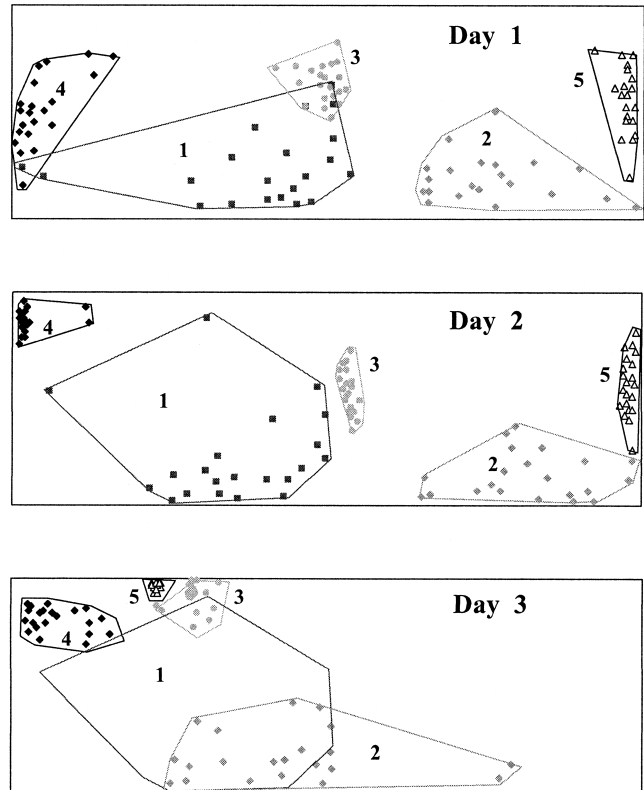

Figure 1
An example of secondary group members' territories in one group aquarium before the removal of the largest secondary member (days 1 and 2) and after its removal (day 3). Note the stability in position before removal and the change in position of the second-ranked secondary group member after removal. For comparison, the outline of the subterritory of the removed individual (from day 2, before its removal) was left in the day 3 figure. Secondary group members are numbered according to size; one is the largest member.

polygon centers for any two group members' polygons (Wilcoxon signed-rank test, $T = 0$, $n = 8$, $p = .01$) (Figure 2b). These differences in overlap and distance also remain significant after a sequential Bonferroni correction (Rice, 1989) was applied to account for multiple testing ($p_{adj} = .02$, and .01, respectively). In our field observations, we found that dominant target group members were significantly closer to the brood chamber than their size-matched subordinates (Wilcoxon signed-rank test, $T = 24$, $n = 15$, $p = .04$) (Figure 3).

Helping behavior

In both the laboratory and the field, position of secondary group members appeared to relate to their helping behavior. In the laboratory, about one third of the secondary group members (16 of 49) took part in helping behaviors during the observation period (Table 1), and there were no significant differences in the frequency of help among different ranks (Friedman's method for randomized blocks for ranks 1–5, df = 4, $\chi^2 = 2.98$, $n = 8$, $p > .5$). Helping behavior in the lab included digging and micronipping. There was no need to defend the territory in the aquarium or to fan the eggs (oxygen level was close to saturation, and fanning behavior is only induced by reducing this level; Keinan, 2001). Our laboratory observations showed that the home ranges of group members who provided help were closer to the brood chamber than the home ranges of those that did not
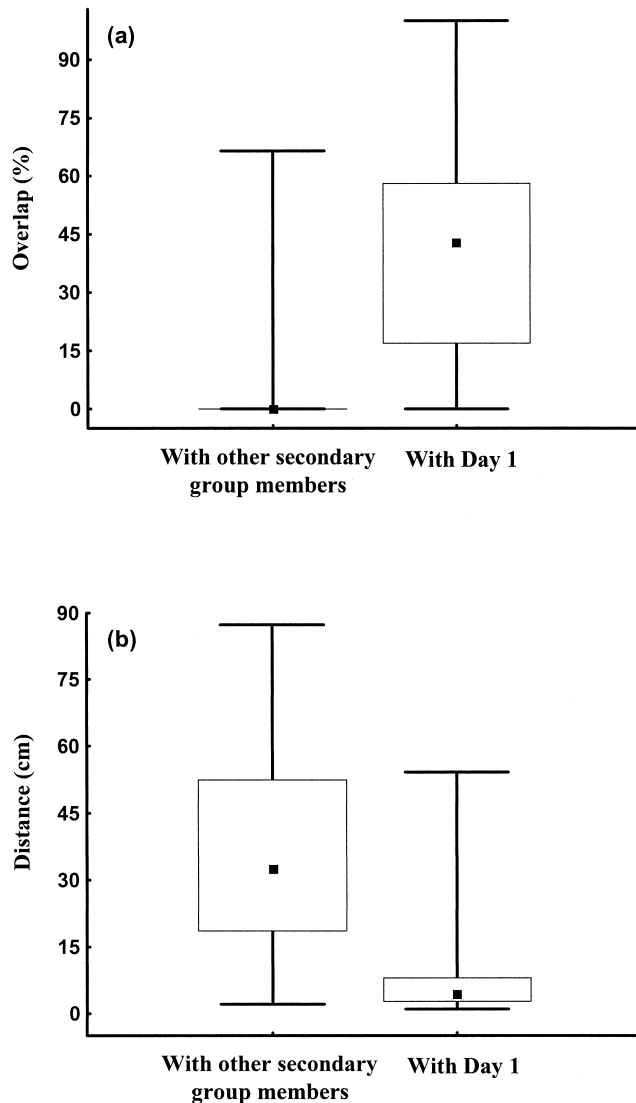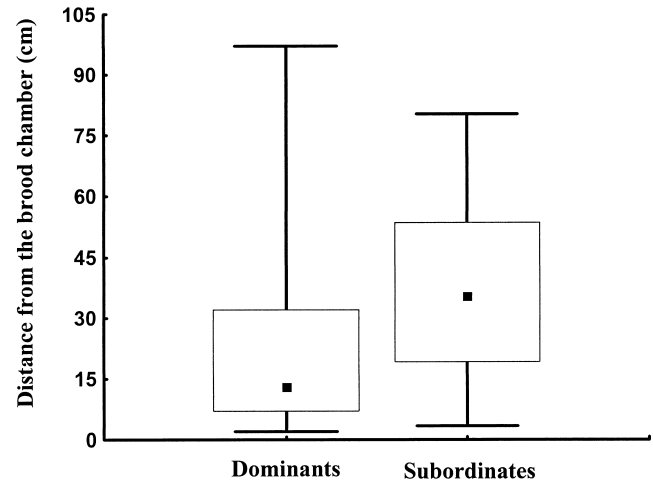
Figure 3
Box-plots of the distance from the brood chamber of dominant and subordinate target individuals observed in the field. Box plots are as in Figure 2.

Figure 2
Box-plots of group means for the following: (a) the average amount of overlap on day 2 between secondary group members' home ranges (left) versus the amount of overlap with secondary group member's own home range on day 1 (right), and (b) the average distance between secondary group members home ranges (see Methods) on day 2 compared (left) to the distance to their own home range on day 1 (right). Black squares inside the boxes denote medians. The upper and lower boundaries of the boxes denote upper and lower quartiles, respectively. Whiskers extend from the upper and lower quartiles to the highest and lowest observations, respectively.

(Wilcoxon signed-rank test, $T = 0$, $n = 87$, $p = .02$) (Figure 4a). In the field, target group members participated in territory defense (Table 2) and territory maintenance and occasionally visited the brood chamber. Target group members that were closer to the brood chamber than were their pair mates (i.e., shorter average distance to the brood chamber; see Methods) spent more time inside it (Wilcoxon signed-rank test, $T = 2$, $n = 15$, $p = .02$) (Figure 4b), and tended to visit it more frequently (Wilcoxon signed-rank test, $T = 8.5$, $n = 15$, $p < .13$) (Figure 4c).

Aggressive interactions among secondary group members

Our behavioral observations, both in the laboratory and in the field, showed that dominance and submission gestures, as well as overt aggression, occur among secondary group members and can easily be observed even during the short time interval of the focal observations (Tables 1 and 2). As might be expected, large secondary group members in the laboratory were more likely to show aggressive displays, whereas smaller group members were more likely to show submissive displays (Friedman's method for randomized blocks for ranks 1–5, df = 4, aggression: $\chi^2 = 13.775$, $n = 8$, $p < .01$; submission: $\chi^2 = 15.025$, $n = 8$, $p < .005$) (Table 1). Multiple comparisons between groups (Siegel and Castellan, 1989) indicated that rank 1 was more aggressive than were ranks 2–5, and ranks 4 and 5 were more submissive than were ranks 1 and 2. In the field, where the two target group members were similar in size (see Methods), there was no apparent difference between them in the level of aggressive and submissive behaviors performed toward all other secondary group members (Wilcoxon signed-rank test, $p < .05$ for all behavioral categories) (Table 2).

Removal effect

If the space segregation described above is a consequence of spatial competition among secondary group members, then a removal of the largest secondary group member was expected to have its strongest effect on the individual next in rank. As expected, in the laboratory experiment, after the largest secondary group member was removed, the individual next in size moved closer to the removed individual's subterritory (the overlap between the territories increased, Figure 5a,b; Wilcoxon signed-ranks test, comparison of day 2 versus day 3: mean distance $T = 1$, $n = 8$, $p = .02$; mean overlap, $T = 0$, $n = 8$, $p = .03$; see also Figure 1). To account for multiple testing of removal effect we applied a sequential Bonferroni correction (Rice, 1989), the change in distance between home ranges remained significant ($p_{adj} = .05$; Figure 5a) and the change in overlap was nearly so ($p_{adj} = .06$; Figure 5b). No significant changes in position were observed for any of the other ranks of group members.

Before the removal, proximity to the brood chamber was associated with helping behavior (Figure 4a,b). Thus, a change in position, similar to that observed after the removal, could have potentially affected helping behavior. However, we did not observe any change in helping behavior by second-ranked

Table 1

Frequency distribution showing the number of times that each secondary group member performed helping, aggressive, and submissive behaviors during focal observations (10 min) in the laboratory, on the second day after spawning

Frequency categories	Secondary group member's rank (based on size)							
	1	2	3	4	5	6	7	8
Helping[a]								
0	3	5	5	7	5	4	2	2
1−10	3		1	1				
11−20		1			1			
>20	2	2	2		2		1	
Aggression[b]								
0		2		4	3	3	2	1
1−5	2	3	7	3	4	1		1
6−10	4	3	1		1		1	
11−20	1							
>20	1			1				
Submission[c]								
0	5	4	1	1		1		1
1−5	3	4	3	2	1	2	1	1
6−10			3	2	6	1	2	
11−20				1	2	1		
>20					1			

[a] Includes digging behavior and micronipping of the eggs and larvae (and was observed in seven of eight groups).

[b] Includes overt attacks and threats, as well as dominance displays, to other secondary group members.

[c] Includes submissive displays and postures to other secondary group members.

secondary group members (Wilcoxon signed-rank test, $T = 1$, $n = 8$, $p = .25$). We did observe an overall drop in helping behavior for all secondary group members from day 2 to day 3 (average number of helping behaviors per individual ± SE = 8.2 ± 2.7 versus 2.5 ± 0.9 for day 2 versus day 3, respectively; Wilcoxon signed-rank test, $T = 8$, $n = 41$, $p = .01$). This temporal fluctuation in helping behavior may have contributed to the fact that removals had no apparent affect on helping behavior by second-ranked secondary group members.

Our behavioral observations also confirm that the removal effect described above is not a result of a change in the behavior of the breeding pair toward the second-ranked secondary group members. There was no difference in the frequency of aggressive behaviors exhibited by the breeders toward first- versus second-ranked secondary group members before the removal (Wilcoxon signed-rank test, $T = 6.5$, $n = 8$, $p = .12$), nor was there a significant change in aggressive behavior toward second-ranked secondary members after the removal (Wilcoxon signed-rank test, $T = 3$, $n = 8$, $p = .58$). The same is true for submissive behavior performed by these individuals toward the breeders. (i.e., no differences between the two ranks before the removal, Wilcoxon signed-rank test, $T = 6.5$, $n = 8$, $p = .12$; and no difference in the submissive behavior of the second-ranked secondary group members before and after removal, Wilcoxon signed-rank test, $T = 4.5$, $n = 8$, $p = .13$).

DISCUSSION

In the laboratory and in the field, secondary group members were aggressive to one another and spatially segregated. In the laboratory, we documented the existence of individual
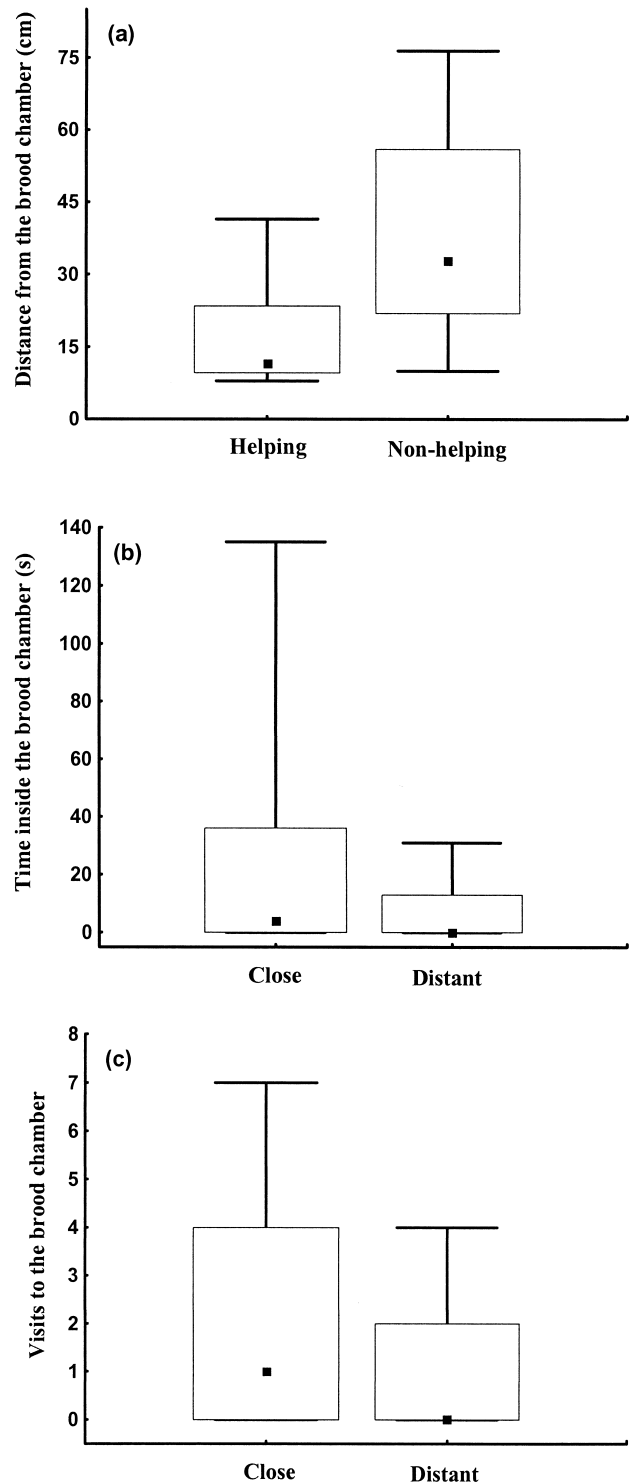

Figure 4
Box-plots of the following: (a) the average distance from the brood chamber for helping versus nonhelping secondary group members in each aquarium (group members were classified as helping if they helped at least once during the observation period), (b) the time spent inside the brood chamber, and (c) the number of visits to the brood chamber by the target individuals in the field observations (the individual closer to the brood chamber versus the more distant one). Box plots are as in Figure 2.

Table 2
The frequency distribution showing the number of times that each secondary group member performed defense, aggression, and submissive behaviors during focal observations (10 min) on the target secondary group members in the field

	Frequency categories	Rank 1	Rank 2
Defense	0	3	6
	1−5	12	9
	6−10	1	1
Aggression given[a]	0	10	9
	1−5	6	6
	6−10	0	1
Submission given[b]	0	10	8
	1−5	6	8
	6−15	0	0
Aggression received[c]	0	15	11
	1−5	1	5
	6−15	0	0
Submission received[d]	0	8	10
	1−5	6	6
	6−10	2	0

[a] Attacks, threats, or dominance displays to other secondary group members (including size-matched group members).

[b] Submissive displays to other secondary group members (including size-matched target group members).

[c] Attacks and threat or dominance displays performed by other secondary group members to the focal individual (including size-matched target group members).

[d] Submissive displays performed by other secondary group members to the focal individual (including size-matched target group members).

exclusive home ranges and found that after removal of a dominant secondary group member, the group member next in rank tended to move closer toward the dominant's former range. In the field, secondary group members also occupied different areas within their group territory, with dominant individuals being closer to the brood chamber. The combination of aggressive interactions and spatial segregation, taken together with the response to the removal experiment, suggests that secondary group members compete for some space-related resource and that such competition leads to space segregation. However, two alternative explanations need to be considered. First, it remains possible that space segregation is caused by parental preference for better potential helpers. Second, it is possible that space segregation emerges because of task differentiation (labor division) among group members. We find these alternative explanations less convincing for the following reasons. (1) These explanations fail to explain the aggressive interactions among individuals. (2) Breeders behaved similarly towards the first- and second-ranked secondary group members before the removal, and did not change their behavior toward second-ranked secondary group members after the removal. Thus, we have no indication that breeders influenced space segregation. (3) In a recent laboratory study on these fish (Keinan, 2001), when the need for help was increased experimentally (by reducing oxygen level and by pouring sand into the brood chamber), only secondary group members with home ranges overlapping the brood chamber responded by increasing their helping behavior. The increase in the need for help did not cause other group members to change their space use. However, other group members did immediately provide parental care (guarding, digging, and carrying) for larvae if the larvae were transferred to their home range. These results suggest that space use by secondary group members is not determined by the need for help, as expected by the task-
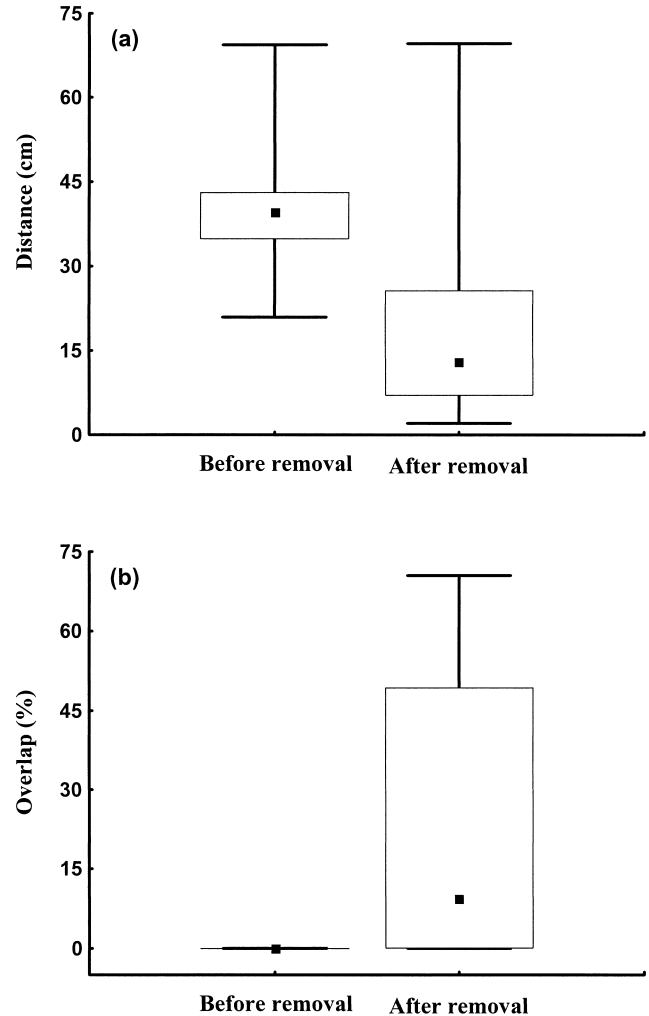

Figure 5
Box-plots of the distance between home ranges (a) and the overlap between home ranges of the first- and second-ranked secondary group members before and after the removal (b, laboratory results) Box plots are as in Figure 2.

differentiation hypothesis, but rather support our suggestion that space use may actually constrain helping behaviors.

One possible implication of spatial competition and exclusion among secondary group members is that it can greatly affect the level of help provided by each individual member. Individuals may be tolerated by the breeders within the group territory and can therefore be viewed as group members, but they may be excluded from the brood chamber by other secondary group members and therefore cannot be viewed as helpers. If the existence of a home range or subterritory restricts an individual's ability to move freely within the group territory, some individuals may be prevented from obtaining access to the brood chamber and helping. This prediction is supported by our data from the laboratory, which showed that the less helpful group members were those located at greater distances from the brood chamber; and by our field observations, which showed that secondary group members who were closer to the brood chamber spent more time inside it. However, the removals, performed in the laboratory, did not affect helping behavior of second-ranked secondary members despite their change of position. This might be explained by the reduced overall helping behavior observed in day 3 (see Results) or, alternatively, by a lower motivation or ability to help by second-rank secondary group members.

As mentioned earlier, the possible effect of competition among secondary group members on their spatial distribution and helping behavior can affect the degree of reproductive skew in social groups. Previous studies on skew have stressed the breeder-helper conflict but tended to ignore possible complications by helper-helper interactions (see Cant, 1998; Johnstone and Cant, 1999; Keller and Reeve, 1994; Kokko and Johnstone, 1999; Reeve and Keller, 1995; Vehrencamp, 1983a,b; but also Johnstone et al., 1999). We suggest that the existence of competition among potential helpers and its effect on the amount of help received by the breeders may influence the benefit of tolerating various individuals in a group and thus may affect the degree of emergent reproductive skew. Similarly, even if secondary group members are allowed a certain amount of reproduction (or take advantage of the breeders' inability to control them), some individuals may have easier access to the brood chamber or to mates than do others. Thus, considering conflicts among secondary group members may be a necessary refinement of reproductive skew theory.

Competition over space among potential helpers may also have implications regarding the origins of helping behavior in these species. Formerly, direct brood care, territorial defense, and territory maintenance were considered helping behaviors in these species (Balshine-Earn et-al., 1998; Taborsky, 1984; Taborsky and Limberger, 1981). However, if helpers occupy individual subterritories within the group's territory and probably have to defend and maintain them, it is not clear whether behaviors such as territorial defense and territory maintenance have necessarily evolved as helping behaviors. Such behaviors could have evolved primarily because of individual benefits from holding a territory and may indirectly be beneficial for other individuals in the group. This may resemble colonial birds that defend their own nest at the edge of the colony and, in so doing, also protect neighboring nests inside the colony. Recently, a similar suggestion regarding sentinel behavior in cooperative breeders (Bednekoff, 1997) received empirical support (Clutton-Brock et al., 1999). Sentinel behavior helps other group members, but the major benefit is gained by the sentinel.

Dominant secondary group members were closer to the brood chamber than were their size-matched subordinates, suggesting that the brood chamber is important to the group members and that they compete over access to the brood chamber. However, we were unable to determine precisely what makes proximity to the brood chamber important. It is clear that the brood chamber is both an excellent shelter and the only place where help can be performed (Taborsky, 1984; Taborsky and Limberger, 1981). Thus, one possibility is that secondary group members compete over access to a better shelter, and variation in levels of helping behavior may be only a by-product of this competition. Another possibility is that helpers compete over the right to help, but this may be predicted only if helping has direct benefits (Carlisle and Zahavi, 1986). Although the latter option is only one way of explaining our results, the evidence for competition among secondary group members found in the present study joins recent theoretical and empirical studies that suggest that further attention should be given to the possible role of direct benefits in the evolution of cooperative breeding (Balshine-Earn et al., 1998; Boland et al., 1997; Cockburn, 1998; Griffin and West, 2002; Heinsohn and Legge, 1999; Lotem et al., 2002; Nowak and Sigmund, 1998; Roberts, 1998).

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