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Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*)

Abstract *Neolamprologus pulcher*, a cooperatively breeding cichlid fish from Lake Tanganyika, lives in permanent social groups comprising one breeding pair and helpers of both sexes. Variation in group size (1–14 helpers) provides an opportunity to investigate factors that affect how many helpers remain in a group and in turn how group size affects reproductive success. This field study showed that larger groups live in larger territories with more shelter. Group size was more strongly correlated with territory quality than with breeder size. Experimental enhancement of territory quality did not affect group size but group size decreased when territory quality was reduced. Breeders living in a large group benefit because such individuals feed more often and have lower workloads and greater reproductive success. Helpers in larger groups also fed more frequently but did not have lower workloads. This is one of the first experimental studies to examine the factors influencing group size in cooperative breeders.

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Introduction

In cooperative breeders, some sexually mature group members care for the offspring of others and do not breed themselves. For the last 30 years, research on cooperative breeding has focused on why such individuals do not disperse and why they help. Surprisingly few studies have examined the factors that determine group size. In many cooperatively breeding mammals and birds, larger groups inhabit better territories and have greater reproductive success (see Brown 1987; Stacey and Koenig 1991 for reviews). These correlations may arise because (1) the best territories are inhabited by the highest-quality parents, (2) only larger groups are able to defend the best territories or (3) only the best territories can support large groups. To determine which of these hypotheses best explains the observed correlation between group size and territory quality, manipulative experiments are needed.

In this study, we examined factors that may affect group size in the cooperatively breeding cichlid, *Neolamprologus pulcher*. This fish (commonly known as the Princess of Burundi) is endemic to Lake Tanganyika, Africa. Family groups of this species defend small territories along the rocky shores of the lake, at depths from 3 to 45 m (Taborsky 1984). *N. pulcher* is small, fast growing (mainly zooplanktivorous) and responds well to experimental manipulations. Individuals from all groups forage together in a large aggregation, feeding on ephemeral patches of zooplankton floating in the water column above the territories. Groups usually contain a single breeding pair, but the number of helpers varies among groups. Helpers share in all aspects of brood care: cleaning and fanning eggs and larvae; defending eggs, larvae and free-swimming young from predators; territory defence (chasing away space competitors) and territory maintenance (removing snails, and digging and carry-

ing sand and debris away from the breeding shelter) (Taborsky and Limberger 1981; Taborsky 1984, 1985).

Although these fish have been studied for many years in Lake Tanganyika, little is known about their dispersal patterns. Helpers are reported to remain in their natal territory until well after they are sexually mature (Taborsky and Limberger 1981; Taborsky 1984, 1985). When a helper disappears from a group, it is difficult to know if that individual dispersed voluntarily, was evicted from the group or was depredated. Only four cases of new helpers joining groups have ever been recorded and on these occasions, the novel helpers were not sexually mature and were medium-sized [around 3.0 cm standard length (SL: total body length–caudal fin)] (S. Balshine, personal observations). An experimental study in the laboratory suggested that helpers prefer to stay in the group but are sometimes evicted by breeders (Taborsky 1985). Helpers are sometimes able to breed in their natal territory by (1) replacing the breeder (Balshine-Earn et al. 1998), (2) sneaking fertilizations (males only) (Dierkes et al. 1999) or (3) spawning with the alpha male in a subterritory on the edge of the natal territory (females only) (Limberger 1983; S. Balshine, personal observations).

Our aims in this study were to examine how the size of groups relates to territory and breeder quality, and to investigate the costs and benefits of group size in terms of individual survival, growth, workload (helping effort) and reproductive success.

Methods

We studied 60 *N. pulcher* families (402 fish) from 17 December 1996 to 9 April 1997, and 177 families (1,199 fish) from 28 January to 7 May 1998. Our study site on the Zambian shores of Lake Tanganyika was located in Kasakalawe Bay, west of Mpulungu and 100 m east of Kasakalawe village. At this site there is a gentle descent to depth and the substrate consists of small rocks mixed with gravel. The families were studied at depths of 7–12 m; observations were recorded on PVC slates while scuba diving. We allowed for a 3- to 5-min habituation period before each observation period. Following the initial habituation period, the fish seemed oblivious to our presence. Preliminary analysis of underwater video footage suggests that the fish are not influenced by the presence of observers.

Family composition and reproductive status (presence of young) was assessed by repeated visits to each family group. Of these families, 99 were studied in great detail (45 groups in 1997 and 54 in 1998). In ten groups, all individuals were temporarily captured (using hand nets and transparent PVC tubes), sexed (by examination of the genital papilla), measured and marked underwater. In the other 89 groups, a minimum of three individuals were captured and marked but all fish (marked and unmarked) could be individually identified by observers based on their territory affiliation, estimates of body length and unique natural body markings. Marking involved injecting non-toxic acrylic paints into the scale pocket (three colours in any combination of 16 possible positions on the body surface). This standard marking technique is non-permanent and does not affect fish behaviour (personal observations). In total, 442 *N. pulcher* were sexed, measured and individually marked (64% of the fish in these families).

Using repeated focal scans and watches, we quantified three factors: (1) territory quality, (2) individual workload and (3) reproductive success (see below for details). There were no statistical differences between the 2 years (Mann-Whitney *U*-tests, e.g.: workload, $z=-0.246$, $n_{1997}=45$, $n_{1998}=54$, $P=0.81$; reproductive success, $z=-0.483$, $n_{1997}=60$, $n_{1998}=177$, $P=0.63$). Therefore, the data from both years were combined.

Is group size correlated with territory quality?

All family members defended a common territory, composed of rocks and sand. Each family's territory was marked with a numbered rock. To investigate whether group size relates to territory quality, we attempted to quantify quality by measuring (1) territory size, (2) number of available shelters and (3) predation intensity.

Size

Using measuring tapes and graph paper we made detailed maps of 60 territories. We used the position where we observed territory disputes between neighbours to define the boundaries of a territory and then we measured the area used by each family. We also counted the total number of neighbours. The total number of neighbours included all *N. pulcher* groups plus all other species that shared a permanent territorial border with our target *N. pulcher* families.

Shelter number

All rocks (larger than 5 cm) in each territory were counted and measured. The median number of rocks per territory (including those used for breeding) was 14 (range 5–33, $n=60$). The rocks in these territories were on average 17×14 cm (range 8–84 cm). One to three rocks in each territory served as the brood chamber in which eggs were laid and tended. By repeat focal watches, we also determined that some other rocks were used as shelter sites (retreats from predators). To ensure easy access, sand and gravel under these shelters (rocks) needed to be excavated. Some family members spent the night in the brood chamber but various family members spent the night in different shelters (individuals appear to always use the same sleeping spots).

Predation pressure (density and survival)

Three times per week, in the morning (0800–1200 hours) and the afternoon (1300–1800 hours), we conducted focal scans, every minute for 3 min, counting the number of predators within a 3-m radius (visually estimated) around a patch of territories. Within the radius scanned there were often several territories; each received the same predator density index. The index was composed of counts from at least six separate visits, and on each visit, three visual counts were taken and averaged for that time of day. No differences in predator frequencies were detected between morning and afternoon scans (Mann-Whitney *U*-test, $z=-1.361$, $n=155,123$, $P=0.17$). Predation risk is related to body length in these fish. Predator counts included species that capture adults or young (e.g. *Lepidiolamprologus elongatus*, catfish, and eels of the family Mastacembelidae) as well as species that specialize on young (e.g. *Gnathochromis pfefferi*). We estimated the frequency of predator attacks from detailed focal watches of 99 families. Whenever witnessed, we recorded predation events, disappearances and signs of injuries believed to be due to predators.

We compared how group size was related to breeder size versus territory quality, and then to tease apart the relative effects of territory versus breeder quality, we performed a multiple regression.

Shelter manipulation experiment

The experiment was conducted from 12 March to 8 May 1998. Of the possible 177 territories available in the study area, we chose

30 that could be matched into trios with similar family sizes. The territories in each trio were randomly assigned to one of three treatments: removal group, addition group and control group. Three shelters (particular rocks used by family members to hide from predators) were removed permanently from the ten territories in the removal group. These removed shelters were placed in the ten territories of the addition group. In control territories, we picked up and immediately replaced three used shelters. The three manipulated shelters represented approximately 50% of the shelters used and 20% of the potential shelters available in the experimental territories. We monitored group size, shelter use and reproductive success (immediately before and then 4 weeks after the manipulations). In each family, we measured the workloads of individuals (helping behaviours: territory defence, territory maintainance and the number of brood chamber visits) and intra-family aggression rates (aggressive behaviours towards other group members, including bites, threat displays, rams, mouth-fights and chases). Estimates were made from four 10-min focal watches (two immediately before and two a month after the manipulation) of the alpha male, the alpha female, and two helpers [one presumed sexually mature helper ≥3.5 cm (Taborsky 1984) and one sexually immature helper <3.5 cm]. To control for temporal variation in behaviour, the matched territories in each trio were observed on the same day and at the same time of day. As matched observations were done concurrently, different observers were involved. Observers switched between the treatment and control groups to avoid observer bias.

Does group size affect workload?

To investigate whether group members in large groups had lighter workloads and thus more feeding time, we measured and compared individual helping behaviour and feeding rates in 99 families. Each individual was observed for 15 min, three times a day (in the morning, afternoon and evening) on at least 2 different days. We defined an individual's workload as its sum contributions to territory defence, territory maintenance and brood chamber activity. Each time an individual was observed to defend the territory (overt and restrained attacks; Taborsky 1984), perform a territory maintenance activity (digging and carrying) or visited the brood chamber, its workload score was increased by one.

Does group size affect reproductive success?

To assess how group size affects reproductive success, all families were visited at least twice a week for the entire field season. We detected newly emerged young in 39 of the 60 families in 1997 and in 95 of the 177 families in 1998. Ninety-two of 134 families had fry in the week before or after the new moon suggesting that there is lunar synchronization of spawning: χ^2-test, $\chi^2=18.6$, $df=1$, $P<0.01$. Whenever newly emerged young were detected, they were counted and subsequently visited every 1–3 days to estimate survival rates. The survival rate was calculated on a per group basis.

To examine the effect of group size on survival rates of young, we considered three family size categories (large: 9–16 individuals, $n=71$; average: 5–8 individuals, $n=102$; small: 3–4 individuals, $n=64$). Survival rates were estimated by calculating the reduction in number of young relative to the number of days between counts. In addition, we investigated whether the initial number of young emerging affected survival rates by calculating the reduction in number relative to the initial number of young observed and the number of days between counts. This survival rate was calculated on a per brood not per group basis.

In our study, most of the data were not normally distributed even after transformation. Therefore, we analysed them using non-parametric techniques, apart from one case. For one analysis, we employed a multiple regression and the data were first successfully normalized with the $\sqrt{x+\frac{3}{8}}$ transformation (see Zar 1984). The results of two-tailed tests are provided unless otherwise stated. We
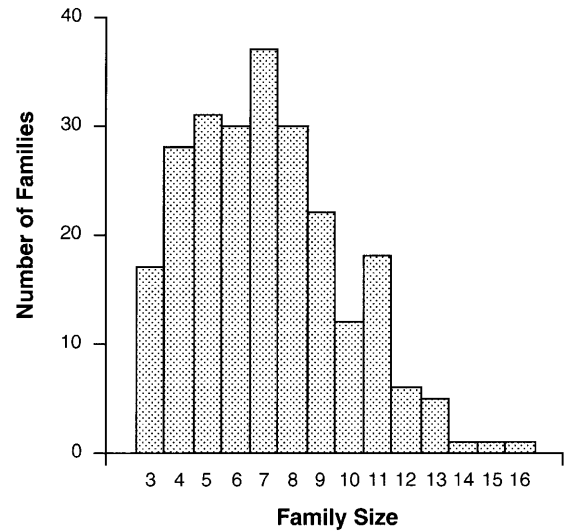

Fig. 1 Distribution of group (family) size in the study ($n=237$ groups of *Neolamprologus pulcher* observed at depths of 7–12 m at Kasakalawe Bay). All individuals ≥2 cm have been included

calculated probability values for Wilcoxon signed-ranks test using the *T*-statistic (see Mundry and Fischer 1998). All values presented are corrected for ties.

Results

N. pulcher families consisted of a breeding pair and an average of five helpers (mean=5, range 1–14 helpers, $n=237$ families; Fig. 1). In our study site, alpha male average body length was 6.0±0.3 cm (SL, mean±SD) while the body length of breeding females averaged 5.2±0.3 cm. Helpers had an average body length of 3.6±1.3 cm (range 2.0–5.7 cm). The male:female sex ratio of captured helpers was 1:0.8 ($n=225$, helper size range that were caught and could be sexed 3.4–5.6 cm).

Group size correlates with territory quality

Size

Larger groups defended larger territories (Spearman rank correlation: $r_s=0.37$, $n=60$, $P<0.003$; one-tailed test). The total number of neighbours was not correlated with family size ($r_s=0.18$, $n=60$, $P=0.21$). The median area used by each family was 3,150 cm², (range 775–10,100 cm²). The median number of neighbors was five (range two to ten).

Shelter number

Larger groups used more shelters ($r_s=0.23$, $n=60$, $P<0.05$; one-tailed test) (Fig. 2). However, controlling for territory size, this relationship disappears ($r_s=0.15$, $n=60$, $P=0.26$). The median number of shelters used per territory was 5 (range 1–14, $n=60$).
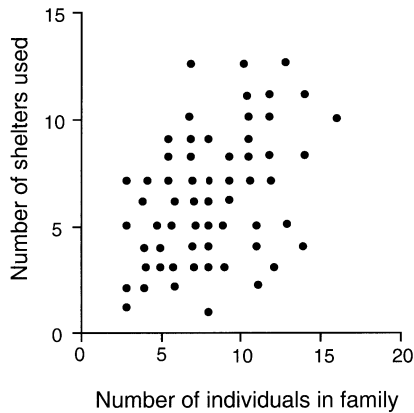
Fig. 2 Number of shelters used by group members versus the number of individuals in each group (*n*=60)

Fig. 3 Median size of groups in which predation on breeders and helpers was observed. The *box plots* show the 25th, 50th and 75th percentiles. The *error bars* represent the 10th and 90th percentiles, and all data points outside this range are plotted

Predation pressure (density and survival)

Larger groups encountered more predators (within a 3-m radius, r_s=0.33, n =237, P<0.0001) and were attacked more frequently (r_s=0.36, n=99, P=0.0004). This could be due to the fact that larger groups are more conspicuous (attraction) or because larger groups live in larger territories which increase the encounter frequency with predators. Individual risk from predator attack (frequency of predator attacks divided by the number of individuals in the group) tended to be lower in larger groups (r_s=–0.17, n=99, P=0.09). During the 2 years of our study, we witnessed a total of 15 predation events (8/390 breeders, a predation probability of at least 0.02 in 7 months for breeders versus 7/1,211 helpers, a predation probability=0.006 for helpers). Helpers rather than breeders tended to be predated in smaller groups (median group size when helper was predated=4), while breeders were predated in average or larger (median group size=7) groups, although not significantly so (Mann-Whitney *U*-test: *U*=43, $n_{breeders}$=8, $n_{helpers}$=7, P=0.10: Fig. 3). In addition, we observed injuries, presumably inflicted by predators, on 14 alpha males, 14 alpha females, 17 large helpers (≥3.5 cm SL) and eight small helpers (<3.5 cm SL). Note that we had reasonable evidence that these injuries resulted from predator attacks and not from territorial disputes or intra-group aggression: the site of injury tends to be on or around the mouth of the fish (as a result of mouth-fighting) for territorial disputes or intra-group aggression, while predators tend to leave marks on the sides of the body. For example, the jaw marks of *Mastacembelus* eels were particularly common and easy to identify.

Territory versus breeder quality

As mentioned in the Introduction, correlations between a good territory (with more space and shelter) and large group size may be due to high-quality breeders holding the best territories. These better breeders may be larger,
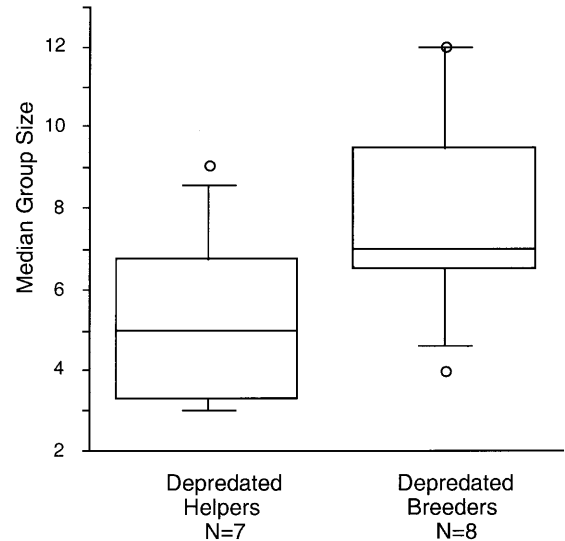
older and/or more experienced parents. In this study, we could only assess the body size of breeders.

The largest male breeders had the most helpers but female size was not related to group size (Spearman rank correlation: males r_s=0.28, n=194, P<0.0001; females r_s=0.04, n=196, P=0.59). As mentioned above, the largest territories had the most helpers. The largest males held the largest territories but female breeder size was not correlated with territory size (males r_s=0.38, n=60, P=0.005; females r_s=–0.099, n=60, P=0.43). To check whether large group size is influenced by a large territory rather than by the size of male breeders, we performed a multiple regression. We found that only territory size was a significant predictor of group size (multiple regression with group size as dependent variable: territory size: t=4.1, n=60, P=0.0002; male size: t=–0.99, n=60, P=0.33).

These correlations indicate that group size was strongly related to territory size (but not breeder quality). Unfortunately, teasing apart cause and effect is not possible. Group size may influence territory size or vice versa. Moreover, territory size is only one measure of territory quality. By changing the number of shelters found in a territory, we experimentally tested whether this measure of territory quality affects group size.

Shelter manipulation experiment

Helper number decreased after shelters had been removed (removal groups) (Friedman test: F_r=11.45, n=10 replicates of three treatments, P<0.005; Fig. 4). Multiple comparisons among treatments showed that (following the manipulations) there was a significant difference in helper number between the addition and removal treat-
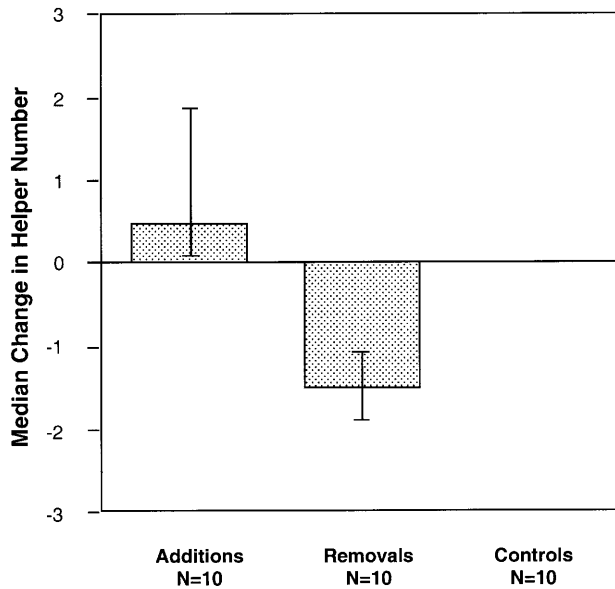
Fig. 4 Median change in number of helpers per family over the experimental period (a comparison of helper numbers before the manipulations and then 4 weeks later). *Error bars* are 25th and 75th percentiles
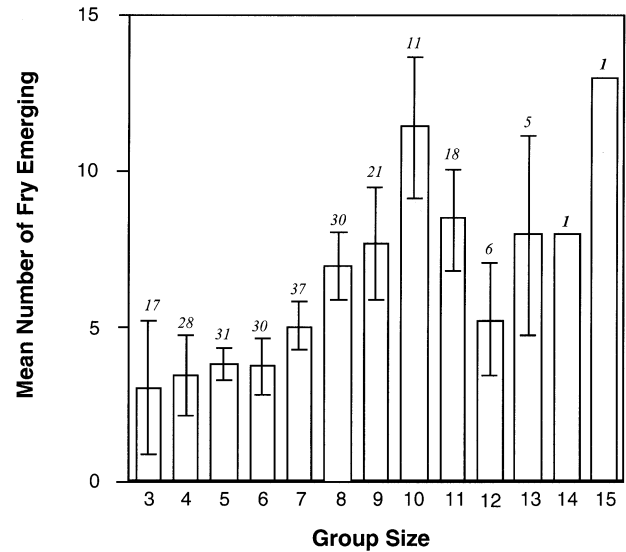

Fig. 5 Reproductive success (number of fry emerging) in families of different sizes (n=237). *Error bars* represent SEs. Numbers in *italics* over error bars are sample sizes. The *bold font* highlights group sizes with a sample size of 1, which may not be representative

ments (see Siegel and Castellan 1988, p. 180; critical value=10.7, $|R_{addition}-R_{removal}|$=14.5, $|R_{control}-R_{addition}|$=4.5, $|R_{control}-R_{removal}|$=10.0).

The number of shelters used, increased significantly in territories to which new shelters were added (F_r=15.2, n=10, P <0.001) but did not change in the removal or control territories (critical value=10.7, $|R_{addition}-R_{removal}|$=16, $|R_{control}-R_{addition}|$=14, $|R_{control}-R_{removal}|$=2). In the control territories, fish continued to use the same shelters; in the territories where shelters had been removed, rocks previously not used as shelters were used as new shelters (these rocks were presumably not used as shelter before the removal because they were of poorer quality).

Following the manipulations, no significant change in territory size was detected among treatments (F_r=0.928, n=10, P>0.50). There was no difference among the three treatment groups in the proportion of families that reproduced (young were observed about 2 weeks after the manipulations in seven addition families, seven removal families and six control families; G-test: G=0.30, df=2, P>0.50).

The workload was similar among all treatments (Friedman test: before manipulations, F_r=3.13, n=10, P>0.20; after manipulations, F_r=1.80, n=10, P=0.50; each type of workload behaviour was given an equal score in this analysis). Workload (brood care, territory defence and maintenance) was measured for each treatment by recording the frequency of brood chamber visits, defence behaviours and digging behaviours of each helper. In all treatments, the workload increased following the manipulations (median workload before=14/10 min, median workload after=18/10 min; Wilcoxon signed-ranks test: z=–2.35, n=30, P=0.02). The observed rise in workload probably reflects the in-

crease in breeding activity following the manipulation (2 families had young before the manipulation whereas 20 families had fry after the manipulation; McNemar change test, c^2=4.08, P<0.05).

Intra-family aggression and submission rates were similar among treatments (Friedman test: F_r=1.8, n=10, P=0.50). Intra-family interactions (aggression and submission) were more frequent after the manipulation (Wilcoxon signed-ranks test:T=118, n=30, P<0.02). In this experiment, both breeders' intra-family aggression rates and helper submission rates were highest in large groups (Spearman rank correlation: breeders, r_s=0.40, n=30, P=0.04; helpers r_s=0.44, n=30, P=0.02).

Group size affects workload

Male and female breeder workloads were negatively related to group size, and breeders' combined workload also decreased with group size (Spearman rank correlation: males, r_s=–0.33, n=96, P<0.002; females, r_s=–0.28, n=94, P <0.01; combined workload for both sexes, r_s=–0.35, n=94, P<0.001). Helper workload did not related to group size (r_s=–0.08, n=170, P=0.36). Breeding females had the heaviest workload (median=9 workload behaviours per 15 min), followed by helpers (median=6) and breeding males (median=4). Individual feeding rates increased with group size (r_s=0.35, n=368, P=0.0006).

Group size affects reproductive success

Larger groups produced more young than smaller groups (Spearman rank correlation: r_s=0.43, n=237, P=0.0001; Fig. 5). We found no evidence that survival rates of

young were related to family size (Kruskall-Wallis test: $H=0.20$, $P=0.91$). The initial number of young emerging did not appear to affect survival rates ($H=1.17$, $P=0.56$).

Discussion

In this study, larger groups were found on larger territories that had more shelter. Breeders in larger groups had lower workloads and produced more young. Manipulations indicated that shelter number influences group size, suggesting that only high-quality territories can support large groups (the third hypothesis mentioned in the Introduction).

Our results do not support the other two hypotheses. Contrary to hypothesis 1 (that highest-quality breeders inhabit the best territories), female body size was not correlated with group size and much less of the variation in group size was explained by male body size than by territory quality. Hypothesis 2 (that only the largest groups can defend the best territories) also appears unlikely. Following shelter removals, group size decreased but the remaining individuals managed to defend the same amount of space. More experimental work needs to be conducted using manipulative experiments on group size to investigate these relationships further.

Stable group size

The theoretical literature on group size emphasizes that stable group size can be viewed as a compromise that reflects the conflicts of interest between insiders and outsiders (Higashi and Yamamura 1993). Our work suggests that the situation is more complicated in cooperative breeders. Three types of players must be considered when analysing group size in cooperatively breeding species: breeders, helpers (group members who may leave or stay) and outsiders (non-group members who may try to join the group). Both extrinsic and intrinsic factors acting on the group will influence the costs and benefits of group expansion or reduction.

Extrinsic factors, such as food availability and territory quality, have been examined in a number of previous studies. Positive correlations have been found between group size and territory quality (Brown and Balda 1977; Woolfenden and Fitzpatrick 1984; Rabenold 1990; Curry and Grant 1991; Nias and Ford 1992). Comparisons among populations have suggested that food availability (Reyer 1984) and shelter number (DuPlessis 1992) influence territory quality and in turn determine group sizes. The results of our study support these findings. In *N. pulcher*, group size appears to be affected by shelter number. Only one other study of cooperative breeders has involved manipulation of territory quality: by increasing the number of roosting sites, DuPlessis (1992) found that group size in green woodhoopoes increases. In our study, a removal of shelters led to a reduction in the number of helpers.

We do not know whether group size decreased because helpers voluntarily dispersed, were evicted or were eaten by predators. However, the first two possibilities are less likely than the third because laboratory experiments have shown that helpers prefer to stay with breeders (Taborsky 1985). In the laboratory (Taborsky 1984) and in the field (this study), each extra helper is beneficial because it reduces the workload for the breeders (and thereby increases feeding time for both helpers and breeders). Therefore, we believe that helpers were probably depredated. We did not observe an increase in helper number in the territories where shelters were added. However, most groups do not reproduce each month and immigrations are rare. Had a longer observation period after the territory enhancement been possible, we may have detected such an increase in group size.

Intrinsic factors (e.g. group dynamics) may also influence group size. Breeders in larger groups practised high levels of intra-family aggression. The high cost of intra-family policing and dominance testing (potential injury and a diversion of energy and time) in larger groups might limit group size.

Different group members are not equivalent: breeders and helpers are likely to have different preferred group sizes (Brown 1987). In *N. pulcher*, breeders should prefer the group to be fairly large because this reduces their workload. Breeders in large groups have more time to feed which increases the number of young produced (in the natural field situation: this study; in a laboratory study: Taborsky 1984). *N. pulcher* helpers may prefer large groups because they can feed more (and grow more quickly). Unlike other studies (Brown et al. 1978; Koenig 1981; Mumme and de Querioz 1985; Farabaugh et al. 1992; Heinsohn and Cockburn 1994), we did not find a reduced workload for helpers in large groups. This result suggests that *N. pulcher* helpers may not pay attention to the effort exerted by other group members. Although helpers in large groups may feed more frequently, their workload is not reduced, and as helpers sometimes inherit the natal breeding spot (Balshine-Earn et al. 1998), they may prefer the group to contain few or no competitors for the alpha breeding spot (same-sexed individuals of a similar size). A conflict of interest over group size and composition between breeders and helpers may contribute to the variation in group size observed in *N. pulcher*. More work is needed to confirm this speculation.

Group size and reproductive skew

Despite the rapid development of reproductive-skew theory for cooperatively breeding animals (Cant 1998; Clutton-Brock 1998; Reeve et al. 1998; Johnstone and Cant 1999; Johnstone 2000), the relationship between group size and the degree of reproductive skew has only very recently been examined (Reeve and Emlen 2000). New work by Rufus Johnstone suggests that if dominants control reproduction, then reproductive sharing be-

tween group members will increase with group size, but if dominants are incapable of controlling subordinate reproduction (incomplete-control models), no clear relationship is predicted between group size and reproductive skew (R. Johnstone, personal communication). We predict that there will be no clear trend between reproductive skew and group size in *N. pulcher* because dominants cannot fully control subordinate reproduction, and helpers of both sexes are known to reproduce both in the laboratory and the field (Dierkes et al. 1999; P. Dierkes, M. Taborsky and R. Achmann, unpublished data). We are currently using microsatellite data to evaluate the degree of reproductive skew in natural *N. pulcher* groups. We shall soon be able to test the two alternative theories by analysing the degree of skew in *N. pulcher* and examining how it relates to group size.

In conclusion, we hope that this paper encourages theoreticians and empiricists to re-examine issues concerning group size and to establish a firm theoretical framework, not just for 'whether' and 'why' but also *how many* individuals should cooperate.

References

Balshine-Earn S, Neat FC, Reid H, Taborsky, M. (1998) Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. Behav Ecol 9:432–438

Brown JL (1987) Helping and communal breeding in birds: ecology and evolution. Princeton University Press, Princeton, NJ

Brown JL, Balda RP (1977) The relationship of habitat quality to group size in Hall's babbler (*Pomatostomus halli*). Condor 79: 312–320

Brown JL, Dow DD, Brown ER, Brown, SD (1978) Effects of helpers on feeding of nestling in the grey-crowned babbler (*Pomatostomus temporalis*). Behav Ecol Sociobiol 13:115–124

Cant MA (1998) A model for the evolution of reproductive skew without reproductive suppression. Anim Behav 55:163–169

Clutton-Brock TH (1998) Reproductive skew, concessions and limited control. Trends Ecol Ecol 13:288–292

Curry RL, Grant PR (1991) Galapagos mockingbirds: territorial cooperative breeding in a climatically variable environment. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds. Cambridge University Press, Cambridge, UK, pp 289–331

Dierkes P, Taborsky M, Kohler U (1999) Reproductive parasitism of broodcare helpers in a cooperatively breeding fish. Behav Ecol 10:510–515

DuPlessis MA (1992) Obligate cavity-roosting as a constraint on dispersal of green (red-billed) woodhoopoes – consequences for philopatry and the likelihood of inbreeding. Oecologia 90:205–211

Farabaugh SM, Brown ED, Hughes JM (1992) Cooperative territorial defense in the Australian magpie, *Gymnorhina-tibicen* (Passeriforms, Cracticidae), a group-living songbird. Ethology 92:283–292

Heinsohn RG, Cockburn A (1994) Helping is costly to young birds in cooperatively breeding white-winged choughs. Proc R Soc Lond B 256:293–298

Higashi M, Yamamura N (1993) What determines animal group size? Insider-outsider conflict and its resolution. Am Nat 142:553–563

Johnstone R (2000) Models of reproductive skew: a review and synthesis. Ethology 106:1–22

Johnstone R, Cant M (1999) Reproductive skew and the threat of eviction: a new perspective. Proc R Soc Lond B 266:275–279

Koenig WD (1981) Space competition in the acorn woodpecker: power struggles in a cooperative breeder. Anim Behav 29:396–427

Limberger D (1983) Pairs and harems in a cichlid fish, *Lamprologus brichardi*. Z Tierpsychol 62:115–144

Mumme RL, Querioz A de (1985) Individual contributions to cooperative behaviour in the acorn woodpecker: effects of reproductive status, sex and group size. Ethology 95:290–313

Mundry R, Fischer J (1998) Use of statistical programs for nonparametric tests of small smaples often leads to incorrect P values: examples from *Animal Behaviour*. Anim Behav 56: 256–259

Nias RC, Ford HA (1992) The influence of group-size and habitat on reproductive success in the superb fairy-wren, *Malurusc yaneus*. Emu 92:238–343

Rabenold KN (1990) *Campylorhynchus* wrens: the ecology of delayed dispersal and cooperation in the Venezuelan savanna. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds. Cambridge University Press, Cambridge, UK, pp 159–196

Reeve HR, Emlen ST (2000) Reproductive skew and group size: an N-person staying incentive model. Behav Ecol 11:640–647

Reeve HK, Emlen ST, Keller L (1998) Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? Behav Ecol 9:267–278

Reyer HU (1984) Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). Anim Behav 32:1163–1178

Siegel S, Castellan NJ Jr (1988) Nonparametric statistics, 2nd edn. McGraw-Hill, New York

Stacey PB, Koenig WD (1991) Cooperative breeding in birds: long terms studies of ecology and behaviour. Cambridge University Press, Cambridge, UK

Taborsky M (1984) Brood care helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. Anim Behav 32:1236–1252

Taborsky M (1985) Breeder-helper conflict in a cichlid fish with brood care helpers: an experimental analysis. Behaviour 95:45–75

Taborsky M, Limberger D (1981) Helpers in fish. Behav Ecol Sociobiol 8:143–145

Woolfenden GE, Fitzpatrick JW (1984) The Florida scrub jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton, NJ

Zar JH (1984) Biostatistical analysis, 2nd edn. Prentice-Hall Englewood Cliffs, NJ