Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*

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Summary

Group size has been shown to positively influence survival of group members in many cooperatively breeding vertebrates, including the Lake Tanganyika cichlid *Neolamprologus pulcher*, suggesting Allee effects. However, long-term data are scarce to test how these survival differences translate into changes in group extinction risk, group size and composition. We show in a field study of 117 groups from six different colonies (three from two populations each), that group size critically influences these parameters between years. Within one year, 34% of the groups went extinct. Group size correlated positively between years and large groups did not go extinct. The latter were more likely to contain small helpers the subsequent year, which is a cumulative measure of the previous months' reproductive success. Finally, there was a tendency that large groups were more likely to contain a breeding male and female still a year after the first check. The breeder male size, breeder female size, and largest helper size did not influence these parameters, and also did not correlate with the sizes these categories of fish after one year. This suggests that group size, and not the body size or fighting ability of group members, was the critical variable determining the success of groups. In total, seven groups had fused with other groups between years. To our knowledge, this is the first study showing long-term benefits of large group size in a cooperatively breeding fish. We discuss the importance of differential survival and dispersal of group members for the demonstrated group size effects.

Keywords: group size, group stability, cooperative breeding, Lake Tanganyika cichlids.

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Introduction

Social animals face a trade-off between the benefits and costs of group-living. On the one hand, individuals may benefit from living in a herd, colony, or group ('aggregations', e.g., Pulliam & Caraco, 1984; Taylor, 1984). Potential benefits include positive effects on survival or reproduction through predator deterrence (e.g., Rasa, 1986; Pitcher & Parrish, 1993; Hill & Dunbar, 1998; Janson, 1998; Clutton-Brock et al., 1999a; Rogovin et al., 2004), sharing in parental duties (Choe & Crespi, 1997; Solomon & French, 1997; Koenig & Dickinson, 2004), and shared vigilance, leaving more time for feeding (e.g., Hailman et al., 1994; Clutton-Brock et al., 2001a, b; Wright et al., 2001; Krause & Ruxton, 2002). On the other hand, individuals face costs of living in aggregations, mainly because of two general reasons. First, aggregations may attract more predators (the 'numerical response', Begon et al., 1990) or they may be more susceptible to parasites (e.g., Moore, 2001). Second, individuals in aggregations may compete for access to resources, e.g. for food (Krause, 1994; Hamilton & Dill, 2003; Bednekoff & Lima, 2004), mates and reproductive opportunities (Davies & Houston, 1986; Goldizen et al., 1998), or shelter (Clifton, 1990; Balshine et al., 2001; Werner et al., 2003).

These counteracting fitness effects are expected to select for an 'optimal group size' (Brown, 1982; Pulliam & Caraco, 1984; but see Sibley, 1983), i.e. the group size where (inclusive) fitness of individual group members is maximised, depending on the ratio of within-group ('local density') and between-group density-dependent effects ('global density') on their fitness, modified by local and global patterns of genetic relatedness (see also West et al., 2002). The decision to join or stay in a group should depend on individuals estimating the net effects of local density and global density on their fitness. Allee (1951) has been among the first to describe this process, whereby at intermediate local densities, the fitness of the group members is being maximised (see also Stephens et al., 1999; Danchin et al., 2001).

A balance between positive effects of living in a group and the conflicts thus arising over access to resources, reproductive opportunities and mates, is likely to pertain also to cooperatively breeding vertebrates (e.g., Taborsky, 1994; Creel & MacDonald, 1995; Cockburn, 1998; Blumstein & Armitage, 1999; Hayes, 2000; Vehrencamp, 2000; Clutton-Brock, 2002; Koenig & Dickinson, 2004). In cooperative breeders, group members share and defend a common territory against other groups. These societies might either

share duties, resources and reproduction in a rather 'egalitarian' way, i.e. all individuals experiencing similar benefits and costs from group-living, or 'despotic', where some group members claim the largest share of benefits at the cost of others (Vehrencamp, 1983). A typical despotic society consists of two dominant breeders, with retained offspring from previous broods assisting their parents raising offspring (Brown, 1987). An egalitarian society has multiple breeder males and/or breeder females sharing reproduction (e.g., Maynard-Smith & Ridpath, 1972; Vehrencamp, 1977; De Luca & Ginsberg, 2001), although usually some group members take a larger share than others based on e.g. age or sized-based dominance hierarchies (e.g., Field et al., 1998; Heinsohn et al., 2000; Widdig et al., 2002; Williams, 2004). Currently, there is an upsurge of interest in when, how, and how much individual group members gain benefits from group living, by using modelling (e.g., Johnstone, 2000; Skubic et al., 2004; Hamilton & Taborsky, 2005), mechanistic (e.g., dominant suppression of subordinate reproduction, Clarke et al., 2001; Clutton-Brock et al., 2001a; De Luca & Ginsberg, 2001) or functional approaches (e.g., when should subordinates disperse and breed independently, Komdeur & Edelaar, 2001; Bergmüller et al., 2005a; Heg et al., 2004a).

We are conducting a long-term study on the behavioural ecology of cooperatively breeding Lake Tanganyika cichlid fish (Taborsky & Limberger, 1981; Heg et al., in press). Our model system is *Neolamprologus pulcher*, a species living in extended family groups, including dominant breeders and up to 20 related and unrelated smaller subordinates or 'helpers' (Taborsky, 1984, 1985; Balshine et al., 2001; Dierkes et al., unpubl. data). Helpers assist the breeders raising offspring, both by direct care (e.g., cleaning and fanning eggs, Taborsky, 1984; Taborsky et al., 1986; von Siemens, 1990) and indirect care (e.g., territory defence, Taborsky, 1984, 1985; Taborsky & Grantner, 1998).

Helpers benefit from group living due to increased survival (Taborsky, 1984; Heg et al., 2004a), but pay costs in terms of reduced growth (and hence probably reduced future competitive and reproductive ability (Taborsky, 1984; Heg et al., 2004b), and risky or energetically costly helping behaviour (Grantner & Taborsky, 1998; Taborsky & Grantner, 1998; Balshine et al., 2001). There is also evidence suggesting helpers pay the breeders for being allowed to stay inside the group (Taborsky, 1984, 1985; Balshine-Earn et al., 1998; Bergmüller et al., 2005a; Bergmüller & Taborsky, 2005). Additionally, some helpers may derive future benefits from group-living, since large

helpers may inherit the territory upon death of the same-sex breeder ('queuing', Balshine-Earn et al., 1998; Dierkes et al., unpubl. data). Finally, helpers may gain inclusive fitness benefits from helping (Taborsky & Limberger 1981; Taborsky 1984). In the Zambian population this benefit is largely confined to small helpers, since genetic relatedness declines exponentially with helper body size (Dierkes et al., unpubl. data).

Breeders benefit from having helpers by increased egg production (Taborsky, 1984), and survival of young (Balshine et al., 2001; Brouwer et al., 2005), and by their own increased survival under the risk of predation (Heg et al., 2004a). These benefits also relate to the breeders having a reduced workload (time spent on parental duties and territory defence) when assisted by helpers (Bergmüller & Taborsky, 2005), as workload correlated negatively with group size for breeders, but not for helpers (Balshine et al., 2001). However, there is also evidence for intra-sexual reproductive conflicts between breeders and helpers (Taborsky, 1985; Balshine-Earn et al., 1998). First, male helpers may parasitise the fertilisation of broods, risking expulsion from the group in the process (Dierkes et al., 1999; Skubic et al., 2004). Male-male conflicts may lead to strategic growth adjustments by male helpers (Heg et al., 2004b; see also Hamilton et al., 2005). Second, female helpers may try to breed polygynously with the breeder male (Limberger, 1983), which may reduce helper assistance of the dominant female's brood. Male and female helpers above a threshold size are reproductively mature, showing little evidence for hormonal suppression of reproductive capabilities (Oliveira et al., 2003). Helpers leave the group and breed independently when given optimal breeding opportunities (e.g., limited competition and no predators), and they may produce a brood already a few days after establishment of an independent territory (Bergmüller et al., 2005a; Heg et al., 2004a). Taken together, these results have shown that delayed dispersal and independent breeding of *N. pulcher* helpers is at least partly explained by the 'ecological constraints' (Emlen, 1982) and the 'benefits of philopatry' hypotheses (Stacey & Ligon, 1991; see also Bergmüller et al., 2005b).

Several publications on group-living in *N. pulcher* have addressed the short-term effects of the (experimentally manipulated) group size and group composition on survival and reproductive success (see references above). The purpose of this paper is to investigate the long-term effects of group size and group composition on sociality in this cooperative cichlid, i.e. on the persistence of groups and on the likelihood of changes occurring in group

composition. We test the hypothesis that group members experience long-term benefits from living in large groups. We marked territories and recorded group composition in the field (March-May 2002). A year later, we relocated these territories and established whether they were still occupied and if so, whether any changes in the group composition had occurred.

Methods

Study site

We studied *N. pulcher* by SCUBA diving at the southern tip of Lake Tanganyika, Zambia, from 5 March - 27 May 2002 and 2 February - 21 April 2003. We studied two populations, each with three colonies (see also Heg et al., 2004a). The first population at Kasakalawe (8°46.849′S, 31°04.882′E) consists of several, partly connected colonies in a sandy area with rocks half submerged in the sand (Balshine-Earn et al., 1998; Balshine et al., 2001). Three colonies at 9.4-11.1 m depth were studied. The second population was located at Nkumbula Island, near Mpulungu. There, *N. pulcher* groups were found hiding and breeding between layers of flat and small round stones, interspersed with patches of gravel and shell debris. Between colonies patches of large boulders (>1 m diameter) could be found, which were not used by *N. pulcher*. In this population, three colonies at 8.5-10.2 m depth were studied. In both populations, shelters were located between and underneath stones and they were maintained by digging away debris (sand, gravel and gastropod shell remains). Groups create a breeding shelter (where eggs are laid on the stone ceiling) and hiding shelters for all group members (where the fish hide from predator attacks, Balshine et al., 2001; Werner et al., 2003). Breeders and large-sized helpers (standard length (SL) larger than ca. 35 mm) preferably forage in the water column (50 to 100 cm above the substrate), where zooplankton is most abundant, but retreat to the breeding and hiding shelters as soon as piscivore predators are approaching.

Study subjects

All groups subjected to experimental treatments in 2002 were excluded from the analyses (Heg et al., 2004a; Brouwer et al., 2005). In 2002, 168 non-experimental group-territories were marked with numbered marker stones

and we determined whether the group contained a breeding male and breeding female(s). Groups were defined according to the home range of the breeding male, and included up to two breeding females ('harems', Limberger, 1983) and up to three patches of stones defended by the male. This definition of 'group' differs from the definition used by Balshine et al. (2001). Since there may be interactions between harem females and helpers of different females or patches, this measure was more conservative in respect to group stability over longer time periods. Time and visibility allowing, the exact group composition was determined (number and size of the breeding male, breeding female(s), helper(s) and free swimming fry). Standard length of each fish was estimated by placing a millimetre board in the territory (0.5 mm classes), and was converted to true SL using a calibration regression line (i.e., estimated SL versus measured SL of a sample of marked individuals). Sigal Balshine and co-workers (2001) showed the body size of the breeder male correlates positively with territory size and thereby influences the group size. An experimental decrease of the territory size by removing shelters immediately reduced the group size (Balshine et al., 2001). Hence, it is conceivable that male size, but maybe also the sizes of the other group members, might have carry-over effects via the territory size on the group size and group composition the next year. Marking and measuring of all group members was not attempted to avoid groups dissolving due to the disturbance (D. Heg & M. Taborsky, pers. obs.). The group members were divided into seven classes for analyses, based on the within-group behavioural interactions and body size: breeder males, breeder females, large helpers (estimated SL > 35 mm), medium helpers (estimated SL = 25.5-35 mm), small helpers (estimated SL = 15.5-25 mm), 'juveniles' (estimated SL = 10.0-15.0 mm) and fry (estimated SL < 10.0 mm). Breeding males were larger than the breeding females and helpers, and most of the breeding females were larger than or at least similar in size to the largest helper in the group.

In 2003, we tried to relocate all groups marked in 2002, by systematically searching the area for marker stones. This was only partly successful, due to marker stones falling down or being turned over or covered with sand. In total, 117 territories marked in 2002 were relocated in 2003 (70%). If still occupied, it was determined whether the group contained a breeding male and breeding female(s). Time and visibility allowing, also the exact group composition was determined and divided into seven classes, as in 2002. We had the following sample sizes: Kasakalawe, colony 2.1: $N = 62$, colony

3.1: $N = 8$, colony 3.2: $N = 24$; Nkumbula, colony 6.1: $N = 17$, colony 6.2: $N = 5$, colony 6.3: $N = 1$.

To add the interpretation of the results, we would like to point out that fry take about 84 days to reach small helper size (15.0 mm SL), about 150 days to reach medium helper size (25.5 mm SL), and about 220 days to reach large helper size (35.0 mm SL, Skubic et al., 2004). Large helpers taking a breeding position can rapidly attain the body size of a typical female (52 mm SL) and male breeder (60 mm SL), due to a rapid increase in growth ('status-dependent growth', see Heg et al., 2004b). This means all fry, small helpers and medium helpers will have outgrown their respective size-classes in-between the two study periods, and some of the large helpers will have attained breeding status (see Stiver et al., 2004). Comparison of the growth data in Stiver et al. (2004, only field data, growth measured after one year) and in Skubic et al. (2004, mostly short-term laboratory measurements) shows growth in the field is ca. 65% of the growth in the laboratory. Taken this difference into account does not alter the above predictions of the helpers outgrowing their size classes, but the number of days to reach a certain size class changes to approximately 129, 231, and 338 days, respectively.

Statistics

We were are not able to reliably mark individuals on a long-term basis without substantial marker loss, so we relied on group size comparisons between the years for our analyses. Using microsatellite markers, both Stiver et al., 2004 and Dierkes et al. (unpubl. data) showed little between-group dispersal of individuals (see also Bergmüller et al., 2005b). Dierkes et al. (unpubl. data) estimated that about 3% of the helpers are immigrants, and if we assume that immigration and emigration rates are independent of group size, this low estimate should hardly affect our analyses. Finally, Brouwer et al. (2005) marked 167 helpers in 2002 within our study population, and none of these migrated to other groups within a two month observation period, and only 3 helpers were missing and presumed dead. Moreover, all the groups studied by Brouwer et al. (2005) were stable, none of the breeders died or left, none of the groups merged with other groups or split into subgroups.

We conducted four major analyses. First, we analysed the probability of group extinction between 2002 and 2003 depending on the group size in 2002, using a Logistic Regression Model with forward selection of terms.

Population and the interaction between group size and the population were added as fixed effects. In a second step, using a sub-sample of groups where we noted the exact group composition, we determined whether group composition modified extinction risk. The effect of body size, standard length of the breeding male, breeding female and the largest helper were entered in this analysis as well. Only the size of largest helper was entered in all analyses, since cooperatively breeding cichlid groups are size-structured (Heg et al., in press; D. Heg and others, unpublished data), leading to positive correlations between, e.g., the size of the largest helper and the second largest helper, third largest helper etc. In case of multiple breeding females within one group, the size of the largest female was selected for analyses. Second, we investigated the effect of group size in 2002, and colony within population effects, on the group size in 2003 using a nested General Linear Model (GLM). Again, in the second step details of the group composition as above were entered, to test for modifying effects on the group size in 2003. Third, we analysed the effects of the group composition in 2002 on the group composition in 2003, using the sub-sample of groups which did not go extinct. Multiple Poisson Regressions were used for this purpose (Crawley, 2002), testing for effects of the group size, the number of breeder females, large helpers, medium helpers, small helpers and offspring in 2002 on the number of breeder females, large helpers, medium helpers, small helpers and offspring as measured in 2003, using separate tests for each 2003 category. Fourth, we established whether the size of the breeder male, breeder female and the largest helper in 2002 allows predictions to be made on the size of these same categories of individuals the year afterwards.

All analyses were conducted using the software SPSS 11.0, except the Poisson Regressions, which were conducted using the software R1.0.8 (Crawley, 2002). The data were over-dispersed in all except one of the Poisson Regression models (Residual Deviance divided by the Residual DF was considerably larger than 1), and we used the F-test, instead of the z-test, to compute statistical significance (see Crawley, 2002, p. 541).

Results

Effects on the group extinction risk

In total, 40 out of 117 groups went extinct between 2002 and 2003 (Kasakalawe: 28.7%, $N = 94$; Nkumbula: 56.5%, $N = 23$). Significantly more groups went extinct at Nkumbula than at Kasakalawe $\chi_1^2 = 6.35$, $p = 0.012$). The likelihood that a group went extinct between 2002 and 2003 was critically depending on the group size in 2002, and corrected for group size, the difference in extinction risk between the two populations was no longer significant (Table 1, Figure 1a). We also analysed the extinction risk for the two populations separately, with colony number and the interaction between colony number and group size as fixed effects. In both analyses, the effect of group size remained positive, but was no longer significant (Kasakalawe: Wald $\chi_1^2 = 2.74$, $p = 0.098$; Nkumbula: Wald $\chi_1^2 = 2.35$, $p = 0.125$), although the slopes for group size for both populations were similar to the overall analysis (coefficients $\pm$ SE, Kasakalawe: 0.154 ± 0.093; Nkumbula: 0.223 ± 0.146; and note that the slopes did not significantly differ from each other: interaction Group size $\times$ Population was non-significant in Table 1). The colony effect and the interaction between colony and group size were non-significant in both populations (Kasakalawe: Wald $\chi_2^2 = 0.30$ and 3.14, $p = 0.84$ and 0.21; Nkumbula: Wald $\chi_2^2 = 2.30$ and 1.84, $p = 0.32$ and 0.40, respectively).

In 92 groups the exact group composition was determined in 2002 ($N = 69$ groups Kasakalawe, 23 groups Nkumbula). We tested whether the extinction risk from 2002 to 2003 was modified by components of the group

Table 1. Results of a logistic regression model on the likelihood of a territory being occupied in 2003, depending on the group size in 2002 (continuous fixed effect), population (fixed effect: Kasakalawe or Nkumbula) and their interaction. Sample sizes were 94 groups at Kasakalawe and 23 groups at Nkumbula.

Independent Variables	Wald χ^2	df	p	Coefficients $\pm$ SE
Constant	0.74	1	0.39	-0.532 ± 0.619
Group size	5.226	1	0.02	0.198 ± 0.087
Population	0.004	1	0.95	-0.081 ± 1.334[*]
Group size $\times$ Population	1.619	1	0.20	-0.167 ± 0.131[*]

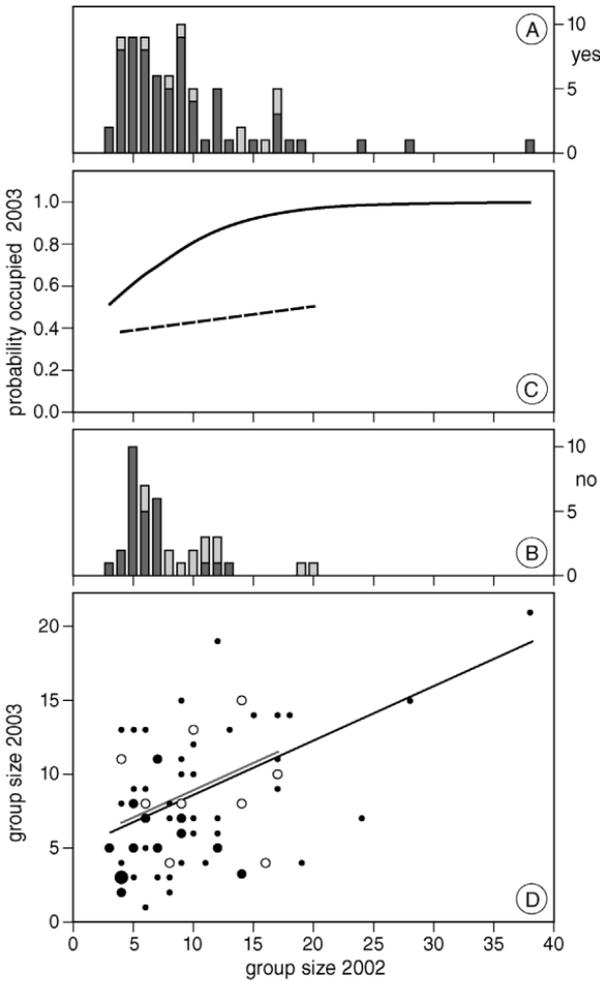[*] Kasakalawe is the reference population and has a coefficient of zero.

Figure 1. The number of *N. pulcher* territories from 2002 that were (a) occupied and (b) not-occupied in 2003, and (c) the resulting probability of occupation in 2003 in relation to the group size in 2002. Kasakalawe population: black bars and line ($N = 94$); Nkumbula population: light bars and dashed line ($N = 23$, see Table 1 for the coefficients of the two logistic regression lines). (d) Group size in 2003 in relation to the group size in 2002. Included are only non-extinct groups. Regression lines are from the model in Table 2. Kasakalawe population: black dots and line ($N = 61$); Nkumbula population: white dots and dashed line ($N = 9$). Overlapping samples from the Kasakalawe population are indicated with increasing symbol sizes (small dots: 1 group, medium dots: 2 groups, large dots: 3 groups).

composition in 2002, but none were significant in a forward selection logistic regression analysis in the model of Table 1 (*p*-values): the number of breeding females (0.96, one or two breeding females in the group), the stan-

dard length of the breeding male (0.38), the standard length of the (largest) breeding female (0.20), the standard length of the largest helper (0.84) and the total number of large helpers (>35 mm SL, 0.64).

Effects on the group size

The group size in 2003 correlated significantly with the group size in 2002 (Spearman $r = 0.40$, $p = 0.001$, $N = 70$, Figure 1b). Using a nested GLM approach, the effect of group size as measured in 2002 on the group size in 2003 remained significant, and was similar between the two populations and the six colonies (Table 2). In 53 non-extinct groups the exact group composition was determined in 2002 ($N = 44$ groups Kasakalawe, 9 groups Nkumbula). We tested whether the group size in 2003 was modified by components of the group composition in 2002, but none were significant when added to the model presented in Table 2 (p-values): the number of breeding females (0.49), the standard length of the breeding male (0.88), the standard length of the (largest) breeding female (0.32), the standard length of the largest helper (0.51) and the total number of large helpers (0.36).

The average group size in 2002 (mean $\pm$ SE $= 8.9 \pm 0.5$, median $= 7$, range $= 3$-38, $N = 117$) was comparable to the average group size in 2003 (mean $\pm$ SE $= 7.9 \pm 0.5$, median $= 7$, range $= 1$-21, $N = 70$, excluding 7 groups were the exact group size could not be determined). We noted that

Table 2. Results of a nested general linear model on the group size in 2003, depending on the group size in 2002 (continuous fixed effect), population (fixed effect: Kasakalawe or Nkumbula), and colony nested within population (fixed effect: three colonies per population).

Independent variables	F	df	p	Coefficients $\pm$ SE
Constant	21.86	1	<0.001	3.78 ± 1.17
Group size	22.75	1	<0.001	0.37 ± 0.08
Population	0.03	1	0.87	2.01 ± 3.87[*]
Colony	0.84	4	0.51	[**]

[*] Kasakalawe is the reference population and has a coefficient of zero. Sample sizes were 61 groups at Kasakalawe (colony 2.1: $N = 37$, 3.1: $N = 6$, 3.2: $N = 18$) and 9 groups at Nkumbula (colony 6.1: $N = 5$, 6.2: $N = 3$, 6.3: $N = 1$).

[**] Coefficients $\pm$ SE for colony 2.1: 0.33 ± 1.08; colony 3.1: 3.14 ± 1.79, colony 3.2:0 (reference); colony 6.1: -1.02 ± 4.16, colony 6.2: -0.70 ± 4.34, colony 6.3: 0 (reference).

the group sizes in 2002 were significantly skewed to the right (Kolmogorov–Smirnov test for normal distribution $z = 1.88$, $p = 0.002$), whereas this was not the case for the group sizes in 2003 ($z = 1.13$, $p = 0.16$). Comparing the group sizes of 2002 and 2003 in a paired design, we detected a significant decline in the group size from 2002 to 2003 (median $= 8.5$ to 7, Wilcoxon's signed ranks test $z = -2.27$, $p = 0.023$, $N = 70$). This might have been due to us only counting the group members in the marked territories for direct comparison with the 2002 data, whereas in 2003 some breeder males had extended their territory boundaries to include extra patches of stones with extra breeder females, or alternatively, adjacent breeder males had taken over the marked group into their own territory. Indeed, we detected seven cases, where two separate focal groups in 2002 were merged in 2003 (18.2% of the 77 groups still existing in 2003), plus one case where one focal group had merged with a non-focal group (1.3% of 77 groups; the non-focal group was marked in 2002, but used in an experiment). Our data do not allow to distinguish between these two processes, but if we add these new group members to give the total group size for the 2003 data (mean $\pm$ SE $= 8.9 \pm 0.7$, median $= 8$, range $= 1\text{-}26$, $N = 63$), we get similar group sizes to the 2002 data (Wilcoxon's signed ranks test $z = -1.51$, $p = 0.13$, $N = 63$). We note that these dynamics in groups and group sizes came about by using the breeder male's territory boundaries as the defining property of a 'group', but we have no evidence to suggest that complete (sub)groups moved to different patches of stones.

Effects on the group composition

Four of the groups still existing in 2003 had lost the breeding pair (5.1%, $N = 77$, all four at Kasakalawe). All other groups had at least one breeder male and one breeder female group member in 2003. An analysis of the effect of group size on the risk of losing the breeding pair was not recommendable using a logistic regression analysis, due to the low sample size of groups without breeders. Nevertheless, non-parametric statistics revealed that small groups tended to lose their breeders more often than large groups: the group size in 2002 of the groups losing their breeders was on average 5.50 (±0.96 SE, median $= 5$, range $= 4\text{-}8$, $N = 4$), whereas it was on average 9.64 in 2002 of the groups who still had breeders in 2003 (±0.70 SE, median $= 8$, range $= 3\text{-}38$, $N = 73$; Mann-Whitney U-test $U = 67.5$, $p = 0.07$). Since

groups without breeders do not produce offspring, the four groups without breeders were discarded from the remainder of the analyses.

One reason why larger groups tend to be large in the next year as well may be due to the positive effects of group size on the reproductive output and survival. Alternatively, some aspect of the group, e.g., the number of breeding females, might be most important for reproductive success, whereas others, e.g. the number of large helpers, might be most important for survival. Such effects might lead to positive correlations between the numbers of different cohorts, whereas other cohort combinations might show no correlations. To test this possibility, the number of juveniles and fry produced were summed into a new variable, the 'number of offspring', because both measures of success were correlated (both years combined, Spearman $r = 0.24$, $p = 0.006$, $N = 132$). Similar to Balshine et al. (2001), we found a significant within-year effect of the group size on the number of offspring, but significant for 2002 only, when we had the largest sample size of groups measured (Table 3). This relationship was also significant when substituting group size with the number of large helpers (Table 3), the number of breeding females (Table 3), the number of medium helpers (Table 3) and the number of small helpers (Table 3), but again in each case only for one year each. Moreover, large groups were not in general 'dominated' by a single size-cohort, instead group size showed positive correlations with all size classes (Table 3).

We also detected between-year effects of the group composition ('carry-over effects'), i.e. the group composition as measured in 2002 correlated with the group composition in 2003 (Table 3). These between-year correlations were less strong than the within-year correlations (Table 3). However, Spearman rank correlations are not very sensitive in detecting these effects. To check whether the group composition in 2002 predicts the group composition in 2003, and whether certain size cohorts were a better predictor than others for certain aspects of the composition in 2003, we also conducted multiple Poisson regressions on the number of offspring, the number of small, medium and large helpers and the number of breeding females in 2003 separately, depending on the group composition of 2002 (Table 4). All the groups remaining in the analysis had one breeding male, so effects on the breeding males were not tested (see above). Controlling for the other effects, the number of offspring in 2003 was, surprisingly, negatively related to the group size in 2002, and positively related to the number of medium and large helpers in 2002 (Table 4). However, since on average groups will increase in size with

Table 3. Spearman rank correlations between components of the group composition. Within-year: comparing the numbers of different types of group members within a year for the data of ($N = 117$, above diagonal) and 2003 separately ($N = 66$ groups, below diagonal). Between-year: comparing the numbers of different types of group members in 2002 (rows) with (columns, $N = 66$ groups), with on the diagonal the correlation between the numbers of members of the same category between years

Number of:	Total group size	Breeding females	Large helpers	Medium helpers	Small helpers	Offspring
Within-year comparisons[a]						
Total group size[c]	–	0.21[*]	0.83[***]	0.76[***]	0.59[***]	0.08
Breeding females	0.31[*]	–	0.24[**]	0.13	−0.04	0.26[**]
Large helpers	0.87[***]	0.13	–	0.43[***]	0.26[**]	0.09
Medium helpers	0.47[***]	0.24[*]	0.15	–	0.39[***]	0.09
Small helpers	0.74[***]	0.11	0.50[***]	0.16	–	−0.04
Offspring	0.30[*]	0.10	0.28[*]	0.06	0.26[*]	–
Between-year comparisons[b]						
Total group size[c]	0.36[***]	0.11	0.30[*]	0.15	0.26[*]	0.21[d]
Breeding females	0.23[d]	0.27[*]	0.09	0.14	0.25[*]	0.08
Large helpers	0.31[**]	0.20	0.23[d]	0.24[d]	0.20	0.26[*]
Medium helpers	0.30[*]	0.01	0.24[d]	0.11	0.22[d]	0.10
Small helpers	0.21	−0.14	0.21[d]	−0.11	0.26[*]	0.02
Offspring	0.26[*]	0.23[d]	0.17	0.24[d]	0.09	0.19

[a] Only groups with one breeder male and at least one breeder female in that year included.

[b] Only groups with one breeder male and at least one breeder female in both years included.

[c] Breeders plus all helpers.

[d] $p < 0.10$, [*] $p < 0.05$, [**] $p < 0.01$, [***] $p < 0.005$.

the addition of medium and large helpers (see the strong within-year correlations between the numbers of the different size classes in Table 3), and the summed positive effects of both helper classes are stronger than the average negative group size effect (Table 4), the overall effect of group size is positive (Figure 2a). The number of small helpers in 2003 was positively related to the number of breeding females and group size in 2002 (Figure 2b). The number of medium helpers in 2003 was positively related to the number of offspring, and tended to be postivily related to the number of large helpers in 2002 (Figure 2c). The number of large helpers in 2003 was positively

Table 4. Significant results of separate Multiple Poisson Regressions, relating components of the group composition of 2003 (dependent variables) to components of the group composition in 2002 (independent continuous variables, all df = 1, N = 66 groups). Depicted are the statistics from F or z tests (F) and the coefficients with standard error (Coeff. ± SE). A dash indicates the effect was not significant (all $p > 0.5$). None of the 2002 components predicted the number of breeding females in 2003 (not shown, all $p > 0.5$).

Dependent Variable (2003)	Large helpers		Medium helpers		Small helpers		Offspring	
Statistic[b]	F	Coeff. ± SE	F	Coeff. ± SE	F	Coeff. ± SE	F	Coeff. ± SE
Independent variables (2002)								
Constant	7.58***	0.930 ± 0.123	−0.68	−0.123 ± 0.182	−3.07**	−1.266 ± 0.413	5.02***	0.964 ± 0.192
Total group size[a]	6.92**	0.026 ± 0.009	–	–	33.4***	0.070 ± 0.010	27.8***	−0.420 ± 0.088
Breeding females	–	–	–	–	4.60*	0.838 ± 0.350	–	–
Large helpers	–	–	1.93†	0.045 ± 0.024	–	–	31.0***	0.523 ± 0.104
Medium helpers	–	–	–	–	–	–	25.7***	0.642 ± 0.130
Small helpers	–	–	–	–	–	–	–	–
Offspring	–	–	2.49*	0.026 ± 0.010	–	–	–	–
Null Deviance (df)	119.1 (65)		69.9 (65)		143.4 (65)		474.6 (65)	
Residual Deviance (df)	112.1 (64)		61.1 (63)		102.1 (63)		437.9 (62)	

Only groups with one breeder male and at least one breeder female in both years included.

[a] Breeders plus all helpers.

[b] Due to over-dispersion F-test instead of z-test used, except for the model on the medium helpers, which was not over-dispersed.

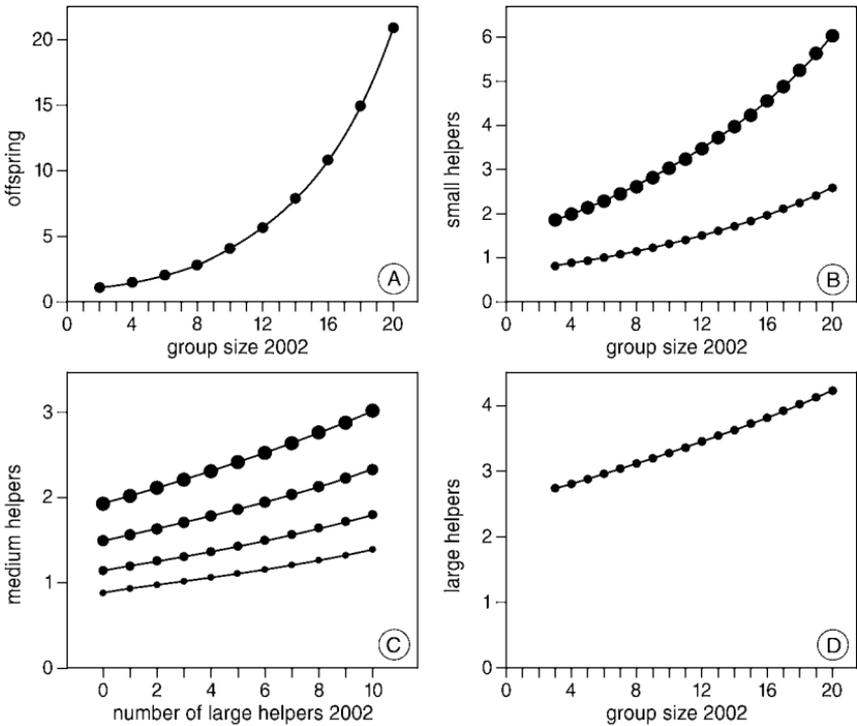† $p = 0.054$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure 2. Predicted numbers of the different group members in 2003 (y-axis) from the group composition in 2002 (Poisson regression curves from Table 4). (a) The number of offspring in 2003 in relation to the group size in 2002, starting with one breeder pair (at 2) and adding one large helper and one medium helper at each step. (b) The number of small helpers in 2003 in relation to group size and one (small dots) or two breeding females (large dots) in 2002. (c) The number of medium helpers in 2003 in relation to the number of large helpers and the number of offspring (0,10, 20 or 30 with increasing symbol sizes) in 2002. (d) The number of large helpers in 2003 in relation to the group size in 2002.

related to the group size in 2002 (Figure 2d). None of the 2002 variables predicted the number of breeding females in 2003, which was not very variable (groups in 2003 with one female $N = 61$, two females $N = 3$, and three females $N = 2$, respectively).

Correlations between the sizes of the large group members

On average, the body sizes of group members were highly correlated, both among breeders (Pearson $r = 0.80$, $p < 0.001$, $N = 114$, data of both years combined), and between the breeder male or the breeder female and the largest helper (Pearson $r = 0.38$ or 0.47, both $p < 0.001$, both $N = 113$,

respectively; one pair of breeders did not have any helpers). Similarly, the body sizes of the breeder male, the breeder female and the largest helper all correlated positively with the current group size (combining the data of both years, Pearson rs = 0.29, 0.35, 0.57, all $p < 0.002$, $N = 114, 114, 115$, respectively).

In contrast, comparing within the same group across the two years, no correlations were detected between the breeder male size in 2002 and the breeder male size in 2003 (Pearson $r = -0.05$, $p = 0.74$, $N = 48$). Similar results were obtained comparing the 2002 with the 2003 data for the breeder females (Pearson $r = 0.08$, $p = 0.57$, $N = 48$) and for the sizes of the largest helper (Pearson $r = 0.15$, $p = 0.30$, $N = 50$). Although positive in direction, there were also no significant correlations between the sizes of the group members in 2002 and the group size in 2003 (Pearson correlations, breeder males: $r = 0.07$, $p = 0.64$, $N = 49$; breeder females: $r = 0.14$, $p = 0.35$, $N = 49$; largest helpers: $r = 0.13$, $p = 0.35$, $N = 50$).

Discussion

Group size and extinction risk

Group size and the presence of helpers has been shown to influence survival and reproduction in *N. pulcher* (Taborsky, 1984; Balshine et al., 2001; Heg et al., 2004a; Brouwer et al., 2005). Our results corroborate these short-term positive effects of group size, suggesting group size also has long-term effects: larger groups were less likely to go extinct and large groups also tended to be large a year later. Positive effects of group size on survival and reproductive success are widespread in cooperatively breeding birds (e.g., Conner et al., 2004; Khan & Walters, 2004; Russell et al., 2004, see also some species listed in Stacey & Koenig, 1990), rodents (e.g., Allainé et al., 2000; Waterman, 2002), carnivores (Rood, 1990; Clutton-Brock et al., 2001b; Courchamp et al., 2002; Russell et al., 2002; see review Russell, 2004), and primates (e.g., Heymann & Soini, 1999; van Noordwijk & van Schaik, 1999), but not always (e.g., Rogovin et al., 2004; Seddon et al., 2004). It should be remarked, however, that the majority of these studies are correlational, i.e. not allowing to distinguish cause from effect (e.g., high quality breeders or territories producing more offspring, and having more helpers as a consequence). But the majority of experimental studies so far

conducted seem to support this general finding (e.g., Brown et al., 1982; Taborsky, 1984; Mumme, 1992; Komdeur, 1994; Brouwer et al., 2005).

Group size was the single most consistent predictor of the group composition of *N. pulcher* the year after first check, i.e. it predicted the number of offspring, small- and large-sized helpers, albeit with a high degree of variation. It should be noted that the total group size, the numbers of breeding females, small-, medium- and large-sized helpers were all highly inter-correlated, suggesting experimental manipulations are needed (see Brouwer et al., 2005), to tease apart short and long-term effects of the different size classes on the group composition. The large residual deviance and the considerable over-dispersion in all except one of our final models, suggests other factors play an important role as well in determining group composition. These may include stochastic breeder and brood loss, perhaps with delayed breeder replacement and productivity, and territory quality (Balshine et al., 2001; Bergmüller et al., 2005a). The number of breeder females present in the group correlated only weakly and non-significantly with the current productivity in the studied groups, but it significantly predicted the number of small helpers one year later. Finally, the current productivity, unexpectedly, only predicted the number of medium-sized helpers (25.5-35 mm SL) the year afterwards, although the published growth rates would suggest that they should rather predict the number of large helpers in the subsequent year. This suggests the natural growth rate of offspring is perhaps smaller than the growth rate reported by Skubic et al. (2004), and even slightly smaller than the growth rate hitherto reported from the field (Stiver et al., 2004, see Methods). Alternatively, the current productivity is an indicator of the group's reproductive potential in the near future, but does not necessarily mean that many of the current brood's offspring will make it to the respective helper cohorts the year after. Clearly, more survival and growth data of the offspring and individually marked small helpers are needed from the field to decide between these two non-exclusive possibilities (Stiver et al., 2004 only report growth data for 14 individual *N. pulcher* between 27 and 63 mm SL). Moreover, it has to be established whether growth rate is affected by the group size in cooperatively breeding cichlids.

Unexpectedly, the body sizes of the breeding males and females, and of the largest helper in the group did not appear to influence the group extinction risk, the group composition and the sizes of these same categories of individuals in the next year, when controlled for group size. On the other

hand, Dierkes et al. (unpubl. data) and Stiver et al. (2004) reported a considerable breeder turn-over rate in this species, particularly of breeder males, i.e. every 200 to 270 days a breeder has been replaced (minimum and maximum estimates of the median territory occupancy based on microsatellite data, see Dierkes et al., unpubl. data). In large groups, the female's breeding position, but not the male's breeding position, is more likely to be inherited by a related female group member, compared to small groups (Dierkes et al., unpubl. data). Given the considerable mortality rates in our study population (Balshine et al., 2001; Heg et al., 2004a), a substantial proportion of individuals will be replaced between years. Any off-balance between the mortality rate, the breeder replacement rate and the (status-dependent) growth rate (Heg et al., 2004b) may lower the correlations between years. Nevertheless, the moderate to high within-year correlations between group size and the sizes of the breeder male, breeder female and largest helper suggests similar sized individuals obtain these respective positions, or grow to sizes similar to the individuals reported the last year due to status-dependent and strategic growth adjustments (Heg et al., 2004b). Studies on marked individuals in the field over prolonged periods of time should solve these points.

Group extinction and the emergence of new groups

We have found a very high rate of group extinction (28.7-56.5%), similar to the high values reported for meerkats *Suricata suricatta* in the Kalahari Germsbok Park, where up to 60% of the groups go extinct after periods of very low rain fall, leading to worsened breeding conditions, and cessation of breeding (Clutton-Brock et al., 1999b). Particularly the smaller groups tend to go extinct, due to positive effects of the group size on adult and juvenile survival in this population (Clutton-Brock et al., 1999a). We did not measure actual survival of marked individual *N. pulcher*, and therefore could not establish whether some individuals actually survived and dispersed to other groups, e.g. after the group has gone largely extinct. Hence, our results are open to three, mutually non-exclusive, explanations. Closely connected to these explanations is the question how new groups come into existence.

First, some groups go completely extinct, without any of the group members leaving the group during the process. Consistent with this explanation is the existence of singles and groups without breeders, also reported for the congener *N. savoryi* (so called 'independents', Heg et al., 2005), suggesting

these groups are in the process of extinction. Maybe in such cases dispersal is not an option for the remaining group members, e.g. due to little survival potential for single individuals and rather low chances to be accepted in another group (Heg et al., 2004a; but see Bergmüller et al., 2005b). Remaining group members might take the risk of staying in the diminished natal group: the largest helpers taking the breeding position (Balshine-Earn et al., 1998) and growing fast to breeder size (Taborsky, 1984; Heg et al., 2004a; Bergmüller et al., 2005a), assisted by the remaining helpers. But if these small groups cannot resume reproduction quickly and successfully to replace the lost group members, the group might still go extinct.

Second, remaining group members might leave the diminished natal group and disperse into neighbouring groups. Consistent with this hypothesis is that emigration of helpers to (mostly neighbouring) groups does occur, albeit rarely, where helpers might either take a helper or a breeder position (Stiver et al., 2004; see also Bergmüller et al., 2005b).

Third, *N. pulcher* groups are less fixed to their respective territories than currently thought, instead groups within colonies are in constant flux due to fusion of small groups with other small groups or with large groups; and fission of large groups. Fusion and/or fission societies are commonplace in primates (e.g., McGrew et al., 1996; Sterck et al., 1997), but have been reported also from other taxa (e.g., Stacey & Koenig, 1990; Heinsohn et al., 2000; Cant et al., 2001; Komdeur & Edelaar, 2001; de Waal & Tyack, 2003). Consistent with this hypothesis is our finding that seven groups of *N. pulcher* had fused during the study period. Fusion means a neighbouring breeding male, sometimes together with some large helpers, starts to visit and assist these groups. Breeders and large helpers take an important share in territory defence against large piscivores (Taborsky et al., 1986), and this might have critically prevented these groups from going extinct. Further, it has been shown that experimentally removed groups were readily replaced by individuals from other groups when inside the colony, but not when at the colony edge (Heg et al., unpubl. data). Heg et al. (unpubl. data) found, first, that some breeder males extended their territory to nearby, experimentally vacated sites, and that large helper females used vacated sites to breed independently (polygynously), sometimes assisted by a couple of dispersing helpers from either the natal group or other groups. Second, experimentally vacated sites more isolated from other groups were taken over by dispersing helpers, sometimes jointly with other helpers from the same group. These

helpers gradually no longer interacted with their natal group members left behind ('fission'). Finally, Dierkes et al. (unpubl. data) found matrilines predominantly in large groups (based on microsatellite genotyping), suggesting long-term stability, whereas smaller groups were more likely to contain individuals that were all completely unrelated to each other (P. Dierkes et al., unpubl. data), suggesting recent fusion events. Nevertheless, our definition of 'groups' was based on the territory boundaries of the breeder males, and we stress here that all field evidence suggests that breeder females and helpers usually remain in their (sub)group, whereas breeder males may change (Balshine et al., 1998). Breeder male replacement may readily lead to fission if the vacancy is filled with two new breeder males or if the new male does not tolerate some of the group members, particularly large male helpers that are unrelated. On the other hand, breeder male replacement may lead to fusion if the vacancy is filled by a neighbouring male extended his territory ('haremic males', see Limberger, 1983).

Conclusions

We conclude that *N. pulcher* gains long-term benefits from living in large groups, consistent with previously reported short-term benefits. However, it remains to be established how many groups go completely extinct due to mortality, due to dispersal or due to both. This suggests we should pay more attention to group size effects on subordinate dispersal behaviour (e.g., see also Field et al., 1999; Kokko & Ekman, 2002; Pasinelli & Walters, 2002; Buston, 2003; Hale et al., 2003). Previous work has concentrated on the benefits of philopatry and ecological constraints hypotheses explaining subordinate delayed dispersal (see review in Koenig & Dickinson, 2004). Incorporating group size effects on the expected future benefits from either remaining in the group and help, or disperse and breed independently, will greatly enhance our understanding of the dynamics of group-living in cooperatively breeding species. For instance, Spinks et al. (2000) found subordinate dispersal increased with group size in mole rats *Cryptomys h. hottentotus* and was in general higher in high-quality 'mesic' habitat than in low-quality 'arid' habitat. They conclude that mesic habitat offers better opportunities for successful new colony formation, for example due to lower costs to find enough food for sustenance (Spinks & Plaganyi, 1999). Ultimately, combining information on group-size dependent reproduction, survival and dispersal will

allow us to predict more precisely when groups are bound to go extinct (the 'lower threshold group size', Courchamp et al., 1999), which is the moment when fusion might become the only alternative to ensure survival. At the same time, it might allow us to predict when it pays large groups to split ('fission') as soon as elevated levels of within-group conflict no longer outweigh the benefits of group-living (above the 'optimal group size', Brown, 1982).

Acknowledgements

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