Experimental global food reduction raises resource acquisition costs of brood care helpers and reduces their helping effort

Rick Bruintjes*, Renske Hekman and Michael Taborsky

Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, CH-3032, Wohlenstrasse 50a, Hinterkappelen, Switzerland

Summary

1. Ecological conditions and constraints are considered to be important for the evolution of cooperative breeding. However, the importance of the costs of resource acquisition to the decision of subordinates to stay or leave and to help or not have been hardly studied experimentally. Here we reduced the overall food availability (zooplankton) for experimental populations of the cooperatively breeding cichlid fish *Neolamprologus pulcher* in the field and measured effects on subordinates' spacing, dispersal, interactions, and helping behaviour.

2. When plankton availability was reduced, all helpers increased feeding rate and moved further away from shelter. Helping correlated negatively with feeding, which suggests a trade-off between foraging effort and cooperation. All group members attacked experimentally presented egg predators later in the food reduction treatment and small helpers in particular decreased their defence effort against them. Furthermore, all subordinates tended to perform less work when food was reduced.

3. This is the first study where food availability was generally reduced in the environment of a cooperative breeder, without affecting the resource distribution between territories. Thereby, our experimental manipulation did not provide dispersal incentives to the test animals, which might have interfered with the decision of subordinates to cooperate. The experimental variation of the costs of resource acquisition for group members revealed significant effects on foraging, spacing, social interactions, and helping behaviour, which highlights the potential importance of ecological constraints on the behaviour, social structure and cooperation propensity in highly social vertebrates.

Key-words: cichlid fish, cooperative breeders, dispersal, ecological constraints, *Neolamprologus pulcher,* social behaviour, spacing, subordinates

Introduction

Ecological constraints have been invoked to explain the evolution of cooperative breeding in animal societies, because they may shift the relative benefits of philopatry and dispersal (Emlen 1982; Koenig *et al.* 1992). The original concept of ecological constraints encompassed everything from a limitation of breeding vacancies to prohibitively high costs of independent reproduction (Emlen & Vehrencamp 1983). However, this provided little predictive power because the degree to which constraints should influence behavioural decisions depends on the nature of the constraint, on many life-history traits and on the type of deci-

sion that has to be made (Stacey & Ligon 1991; Hatchwell & Komdeur 2000; Kokko & Ekman 2002). Therefore, to understand the importance of ecological constraints for optimal behavioural and life-history decisions of group breeding animals, two different levels need to be specified: (i) the type of constraint and (ii) the type of decision. Ecological constraints fall into one of three categories; (a) habitat saturation, which can directly affect opportunities of dispersing individuals to breed independently (Komdeur *et al.* 1995); (b) mortality risk, which can affect dispersal decisions if philopatry means survival becomes more likely (Heg *et al.* 2004); and (c) costs of resource acquisition, for instance food, which can affect dispersal decisions if resource variance has a strong regional component (Dickinson & McGowan 2005). The decisions subordinate group

*Correspondence author. E-mail: rbruintjes@yahoo.com

members need to make concern (a) whether to stay in the group or leave (Walters, Copeyon & Carter 1992); and, if they stay, (b) whether to help raising the offspring of dominants (Eden 1987; see Stacey & Koenig 1990 for reviews).

The decision to stay or leave can be influenced by all three types of constraints, because the fitness consequences of philopatry and dispersal may differ considerably subject to all of them. Exact predictions about the direction and magnitude of the influence depend on specific life-history traits involved and on related population dynamics (Pen & Weissing 2000; Kokko & Lundberg 2001; Kokko & Ekman 2002). Regarding the decision to help or not, there is no reason to expect a direct influence of habitat saturation, because if anything, this decision should depend on the conditions within rather than outside the home territory; cooperation will be indirectly affected through decisions to stay or leave, because help is only feasible if subordinates stay in the group. Furthermore, the decision to help should be influenced by mortality risk if a pay-to-stay scenario applies (Gaston 1978; Kokko, Johnstone & Wright 2002), i.e., if helpers are subject to reduced survival chances if they leave the group (Taborsky 1984, 1985; Heg *et al.* 2004). Finally, helping decisions should directly depend on the costs of resource acquisition as a result of possible effects on (i) helping potential, and (ii) the trade-off between current and future fitness gains (Canestrari *et al.* 2008). The latter holds especially if current environmental conditions allow predicting future conditions.

Few studies have yet addressed the question of how the costs of resource acquisition affect helping decisions in cooperative breeders. In this context it is important to distinguish between global and local variation of resource availability. For example, if the environmental quality is bad overall (global condition), there may be no incentive to leave the home territory, so the decision to help or not can be investigated largely independently from the philopatry question. In contrast, if the environmental quality varies greatly between areas (local condition), the decision to stay or leave the home territory may be of primary importance, which interferes with the decision to help (Covas, Doutrelant & du Plessis 2004; Bergmüller, Heg & Taborsky 2005a; Lucia *et al.* 2008) hampering the possibility to make clear predictions about experimental effects on helping levels.

In different species of birds and mammals, experimentally amended habitat quality on a small or local scale was shown to affect cooperation. Helping behaviour of subordinate group members was increased by food augmentation in the home territory of moorhens (*Gallinula chloropus*: Eden 1987), white-winged choughs (*Corcorax melanorhamphos*: Boland, Heinsohn & Cockburn 1997), Arabian babblers (*Turdoides squamiceps*: Wright & Dingemanse 1999), meerkats (*Suricata suricatta*: Clutton-Brock *et al.* 2002) and carrion crows (*Corvus corone corone*: Baglione *et al.* 2006; Canestrari *et al.* 2008; but see Canestrari, Marcos & Baglione 2007), which shows that helpers respond to the costs of local resource acquisition. However, to our knowledge cooperation responses of subordinate group members to environmental manipulation were hitherto neither tested in a food reduction

paradigm, nor by resource manipulation on a global scale. This is an important gap, because experiments with food reduction rather than augmentation would allow a more direct test of the effect of limitations (i.e., tight constraints); and, as outlined above, experimental manipulation of global conditions should allow to test for effects on helping propensity largely independently of the decision to stay in the group or to leave. In addition, the conditions outside of the home territories of helpers should influence their spacing behaviour, social interactions and helping contributions (see Komdeur 1992; Bergmüller, Heg & Taborsky 2005a). Hence, the different spatial scales of local and global food manipulation create different predictions for spacing, dispersal and helping behaviour in cooperative breeders.

Here we tested for effects of a reduction of global food availability on foraging, spacing, social interactions, and the decisions to help and to disperse, of subordinate group members in the cooperatively breeding cichlid *Neolamprologus pulcher*. Groups of this species consist of a breeding pair with their offspring and on average 5 to 8 helpers of different sizes, including immature and mature males and females (Taborsky & Limberger 1981; Balshine *et al.* 2001; Heg *et al.* 2005). Helpers participate in territory defence, brood care and territory maintenance (Taborsky 1984). Breeders and helpers feed mainly on zooplankton outside of their home territory (Taborsky & Limberger 1981; Gashagaza & Nagoshi 1986). By digging away sand, these fish create distinct patches of stones that provide shelter for hiding and breeding (Balshine *et al.* 2001; Heg *et al.* 2008). As a result of a high breeder turn-over rate and because helpers stay in the territory when breeders are replaced, the relatedness of helpers to beneficiaries decreases with age (Taborsky & Limberger 1981; Dierkes *et al.* 2005). Consequently, helpers help to raise non-kin broods and therefore kin selection alone cannot explain cooperative behaviour in this species (Taborsky 1984; Brouwer, Heg & Taborsky 2005). Instead, helping behaviour of large subordinates seems to serve as payment to remain tolerated in the territory (Taborsky 1985; Balshine-Earn *et al.* 1998; Bergmüller, Heg & Taborsky 2005a; Bergmüller & Taborsky 2005; Bruintjes & Taborsky 2008). Furthermore, *N. pulcher* helpers have been shown to increase the productivity of breeders (Taborsky 1984; Taborsky, Skubic & Bruintjes 2007) and to reduce their work load (Balshine *et al.* 2001; Bergmüller & Taborsky 2005); additionally, they raise the survival probability of the breeders' offspring (Brouwer, Heg & Taborsky 2005), which is partly responsible for a positive correlation between helper number and reproductive success (Balshine *et al.* 2001), and for group stability (Heg *et al.* 2005).

We tested the response of group members to experimental variation of global food availability in a natural breeding colony of *N. pulcher* in 16 large underwater cages including 2 to 3 group territories each. The space available in these cages roughly covered the natural home range of the experimental fish. We encased half of the cages with fine-meshed plankton nets that reduced the plankton flow, whereas the other half remained uncovered to serve as control. This food reduction

was intended to reflect natural fluctuations of zooplankton availability, as the food availability was reduced uniformly for all group members. We predicted that the resulting change in the costs of resource acquisition would entail the following:

1. Increased opportunity costs because of increased feeding effort; group members would have to move further and spend more time foraging if the food source was impaired;
2. No effect on dispersal, because food is mainly consumed outside of territories and therefore territory quality is uncorrelated with food availability in this species; more generally, results of modelling effects of constraints on dispersal decisions of subordinate group members suggest that environmental constraints as such have limited predictive power, because they interact with many life-history traits that can have opposing effects on dispersal behaviour (Kokko & Lundberg 2001);
3. Reduced helping behaviour because of increased opportunity costs, particularly in group members disposing of little reserves (i.e., small, immature group members, which dispose of significantly poorer body condition in the field; F. Neat, S. Balshine & M. Taborsky, unpublished data). We did not expect an *increase* of helping based on a decision to prioritize current over future fitness (cf. Canestrari *et al.* 2008), because current variation in zooplankton availability does not allow to predict future levels. In addition, helping of large subordinates apparently serves mainly to pay rent (Bergmüller & Taborsky 2005), so the current fitness of large helpers will not be directly affected by varying helping levels, but only by their interactions with dominants.

Materials and methods

STUDY SPECIES

Neolamprologus pulcher occurs in the sublitoral zone all around the shores of Lake Tanganyika (Duftner *et al.* 2007). We studied *N. pulcher* by SCUBA diving at 8·5–11 m depth at Kasakalawe point at the southern end of Lake Tanganyika, Zambia (8°46·849'S, 31°04·882'E) from September to November 2005. Breeders and large-sized helpers forage in the water column at an average height of 60 cm (up to 175 cm) above the substrate and feed predominantly on zooplankton; small fish sporadically feed on benthic invertebrates as well (Gashagaza 1988). A detailed description of the social structure and behaviour of *N. pulcher* in this population has been given elsewhere (Balshine-Earn *et al.* 1998; Balshine *et al.* 2001; Stiver *et al.* 2004; Bergmüller *et al.* 2005b; Brouwer, Heg & Taborsky 2005; Dierkes *et al.* 2005; Heg *et al.* 2005, 2008; Dierkes, Taborsky & Achmann 2008). Group territories were marked with numbered stones and mapped. Group compositions were determined by repeated focal group observations. All data were recorded underwater with soft pencil on PVC-slates.

EXPERIMENTAL SET-UP

Experimental units were created by selecting haphazardly two to three adjacent group territories located within 1–1·5 m of each other. Each unit consisted minimally of two group territories and each group was minimally composed of a male and female breeder, one small helper [25–35 mm standard length (SL)] and one large helper (> 40 mm SL). The mean group size was 7·6 ± 1·9 individuals > 15 mm SL. Then a cage (size: 2 × 2 × 2 m; aluminium frame covered with a sturdy plastic net, mesh size 2·5 × 2·5 mm to allow free plankton flow) was placed over the selected units and all medium and large piscivores were removed (see Heg *et al.* 2004 for description of a similar experimental set-up).

Per trial (*n* = 8) two cages were placed in close vicinity of each other to minimise locality effects including habitat structure, plankton flow and species composition. One of the two cages of each replicate was randomly assigned as the control and the other cage was covered with a plankton reduction net (*n* = 16 cages including 33 groups in total; two groups per cage were used for focal observations, rendering 32 focal observation groups; see below for observation details).

The presence of helpers of different sizes per group was assured as different sized helpers show different helping repertoires (Bruintjes & Taborsky 2008). Furthermore, helpers become sexually mature at approximately 35 mm SL (Taborsky 1985), which might change their propensity to cooperate. One to four helpers per group were caught with help of transparent tubes and hand nets, sexed, measured (SL in mm, accuracy 0·5 mm), and individually marked by carefully excising half of a single fin ray of the dorsal fin. To minimise disturbance, only individuals with a similar size to other group members were caught and marked to facilitate identification.

The cages contained the entire environment the focal group members would usually use and were sufficiently large as the natural territory area of a group is on average only 0·315 m² (range 0·078–1·010 m²; Balshine *et al.* 2001). Observations were done through two doors (60 × 80 cm) equipped with zippers and located 35 cm from the bottom at opposite sides of the cage. The polyester plankton reduction nets that were pulled over the cages had a mesh size of 250 μm and doors with zippers matching the cage doors. Each trail lasted 2 weeks.

To measure the effect of the experimental plankton reduction we collected plankton samples after performing behavioural observations by hauling a plankton net (inner mouth diameter: 17·8 cm; length: 117 cm; mesh size: 100 μm) horizontally back and forth inside the cages for a total stretch of 8 metres at 45–55 cm height from the bottom. The samples were washed out, collected with a sieve (100 μm) and stored in 95% ethanol prior to classification and quantification with help of a microscope. The sampled items were divided into five equidistant size classes (see Appendix S1 in Supporting Information for size categories and taxa).

BEHAVIOURAL RECORDINGS

The fish in the control and plankton reduction cages showed no signs of stress and the food intake rates were comparable to *N. pulcher* outside the cages (200–400 plankton bites per 15 min) and to previously reported data (Balshine-Earn *et al.* 1998; Heg *et al.* 2004). During each replicate, one small and one large focal helper of two groups per cage were observed in random order three times for 10 min each, evenly distributed over the treatment period. In total 32 territorial groups were observed between 8:30 h and 17:00 h, producing 192 focal observations. All behaviours were recorded in frequencies of occurrence, except time spent inside the breeding shelter, which was measured in seconds with a stopwatch.

Recorded behaviours include overt attacks (ramming, biting, mouth fighting), restrained aggressive displays (frontal approach, head-down display, S-shaped bending, head jerking, opercula

spreading, raising dorsal fin), submissive behaviour (tail quivering, hook display, fleeing) territory maintenance (digging, i.e. carrying sand out of a shelter) and feeding (plankton or benthos). Effort of helpers was calculated as the sum of all helping behaviours performed including territory defence (all overt attacks and restrained aggressive displays against non-family members and heterospecifics, territory maintenance and all breeding shelter visits; see Balshine *et al.* 2001).

EGG PREDATOR AND SAND EXPOSURE

During the experiment, every group was exposed twice to experimental sand addition and egg predator trials to acquire a standardised estimate of the helping propensity. In the egg predator trials a *Telmatochromis vittatus* (mean SL ± SE: 33·22 ± 2·49 mm, $n = 17$ different individuals) was presented for 10 min in a clear Plexiglas presentation tube (length 15 cm, inner diameter 8·2 cm) at 5 cm distance from the breeding shelter entrance. These syntopic cichlids are opportunistic egg predators. We recorded the latency to first attack, by which group member it was performed, all aggression against the *T. vittatus* from all group members, and the activity level of the exposed intruder on a scale from 0 to 5 (0 = no activity, 5 = very active). Neither the size of the *T. vittatus* nor their activity differed between the treatments (size: *t*-test, $t_{48} = -0·116$, $P = 0·908$; activity: Mann–Whitney *U*-test, $z_{66} = -1·050$, $P = 0·294$).

In the sand addition trials, the breeding shelter of the target group was carefully half-filled with sand to induce digging behaviour (this simulates natural conditions created by water movements after a heavy surge; Taborsky & Limberger 1981). The 10 min recording of digging behaviour started after the first individual of the group began to dig, or after 5 min if no digging was shown until then. We recorded latency to first digging, by which individual it was performed, and all frequencies of digging per group member. All behaviours shown in the sand and egg predator trials were analysed per capita.

HELPER SPACING AND DISPERSAL

During the behavioural observations described above, the focal helpers' locations were determined by estimating their height in the water column and the distance from the breeding shelter once every minute for all 10 recording minutes. Before the experiment started, every cage was equipped with a dispersal shelter consisting of stones and empty snail shells in an unoccupied corner of the cage, between 0·5 and 1·5 m from the group territories. The dispersal shelter was constructed to allow helpers to disperse and breed independently. Previous studies showed that individuals preferentially disperse to neighbouring territories (Stiver *et al.* 2004; Bergmüller *et al.* 2005b; Heg *et al.* 2008). The dispersal territories were checked once every week for occupancy during 20 min observations. Individuals were considered to have dispersed if they occupied and defended the dispersal shelter (see Heg *et al.* 2004).

STATISTICS

All data were analysed using SPSS software (versions 11.5 & 13.0, SPSS Inc., Chicago, IL, USA). We checked for normality with the one-sample Kolmogorov–Smirnov test. Means of the three observations per focal helper were calculated and if necessary, data were normalised by logarithmic or square root transformations. Normally distributed data were analysed using GLMM, with treatment and helper size as fixed effects, group nested in cage, cage, group and observer as random effects, and time of observation, date and number of fish present in the group (> 25 mm SL) as covariates. Non-significant (interaction) effects, non-significant covariates and redundancies ($P > 0·250$) were discarded from the statistical model. However, treatment, helper size and the interaction effect treatment*helper size always remained in the model. Normally distributed overall effects, where the treatment was not considered, were analysed with paired-sample *t*-tests. Otherwise, Wilcoxon matched-pairs signed-ranks tests were used for paired data. Correlations were tested with Pearson's correlation analyses if data were normally distributed and the variances were homogeneous, otherwise we used Spearman's rank correlation analyses. Multiply tested data were controlled for false discovery rates (Verhoeven, Simonsen & McIntyre 2005).

Results

PLANKTON AVAILABILITY

The plankton reduction net significantly reduced the zooplankton number (*t*-test: $t_{12} = 2·460$, $n = 14$, $P = 0·030$). On average there were 56% less invertebrates per tow in the plankton reduction treatment than in the control group (plankton reduction group [mean ± SE]: 41·9 ± 17·1 invertebrates; control group: 74·2 ± 30·3 invertebrates).

FORAGING

The total number of plankton bites was significantly higher for large and small sized helpers in the plankton reduction treatment compared with the control, whereas no helper size effects were found (Table 1).

Small helpers had a larger benthos intake rate in the control than in the plankton reduction treatment, while in large helpers benthos feeding did not differ between treatments (treatment effect small helpers alone: *t*-test: $t_{30} = 2·500$, $P = 0·018$; treatment effect large helpers alone: $t_{30} = 0·243$, $P = 0·810$). In the plankton reduction treatment there was a significant negative correlation between the number of plankton and benthos bites (Pearson correlation: $r_s = -0·424$, $n = 32$, $P = 0·016$), whereas no relationship was found in

Table 1. Results of two separate GLMMs, testing for fixed effects of the treatment, helper size and their interaction effects on the total number of plankton and benthos bites

Dependent variable, Independent variables	GLMM without distance		
	F	df, error df	*P*
Total Number of plankton bites			
Treatment	6·32	1, 11·1	**0·029**
Helper size	0·01	1, 37·3	0·959
Treatment × helper size	0·35	1, 39·7	0·560
Total Number of benthos bites			
Treatment	2·27	1, 14·0	0·154
Helper size	0·17	1, 30·0	0·685
Treatment × helper size	3·45	1, 30·0	<u>0·073</u>

Significant *P*-values are highlighted in bold and the underlined *P*-values are between 0·05 and 0·10.

the control treatment (Pearson correlation: $r_s = -0.076$, $n = 32$, $P = 0.680$). In the control treatment the amount of invertebrates caught per plankton tow correlated positively with the total plankton uptake for large helpers (Spearman rank correlation: $r_s = 0.841$, $n = 6$, $P = 0.036$), but not so for small helpers ($r_s = 0.432, n = 7$, $P = 0.333$).

SOCIAL INTERACTIONS

Small helpers received less aggression from members of their group in the plankton reduction treatment than in the control treatment (Mann-Whitney U-test, $z_{32} = -2.052$, $P = 0.040$) and the amount of received submission tended to be higher for small helpers in the plankton reduction treatment than in the control treatment (Table 2); almost 90% of this submission was received from juvenile helpers (15–25 mm SL). The quantity of aggression and submissive behaviour performed

Table 2. Results of a GLMM of the total helping effort, and the results of treatment effects on the amount of intra-group aggression, defence [aggressiveness towards other species and conspecifics not belonging to the own group], submissiveness and frequency of digging for large and small helpers together, separately and overall [i.e. for both treatments combined]. (All data except the total helping effort were tested with Mann-Whitney U-tests and multiple tested data were controlled for false discovery rates)

	Statistic		Significance
Total Helping Effort	F	df, error df	P
Treatment	3·817	1, 41·0	0·060
Helper size	0·517	1, 41·0	0·478
Treatment × helper size	1·396	1, 41·0	0·247
Large & Small Helpers	z		P
Aggression	0·424		0·672
Received aggression	1·329		0·184
Defence	0·296		0·767
Submissiveness	0·833		0·377
Received submissiveness	1·180		0·238
Digging	0·957		0·338
Small Helpers			
Aggression	0·294		0·769
Received aggression	2·052		**0·040**
Defence	0·132		0·895
Submissiveness	0·447		0·655
Received submissiveness	1·878		0·060
Digging	0·128		0·898
Large Helpers			
Aggression	0·690		0·490
Received aggression	0·105		0·916
Defence	0·831		0·406
Submissiveness	0·770		0·441
Received submissiveness	0·348		0·728
Digging	1·386		0·166
Large vs. Small Helpers (overall)			
Aggression	0·245		0·807
Received aggression	0·814		0·416
Defence	0·461		0·645
Submissiveness	2·469		**0·014**
Received submissiveness	1·494		0·135
Digging	2·043		**0·041**

Significant *P*-values are highlighted in bold and *P*-values between 0·05 and 0·10 are underlined.

towards own group members did not differ between treatments, but small helpers were generally more submissive towards group members than large helpers were (Table 2). When data of large and small helpers were pooled, neither intra-group aggression nor submission spent and received differed between the treatments (see Table 2).

HELPING BEHAVIOUR

The total helping effort tended to be higher in the control treatment than in the plankton reduction treatment, whereas helper size had no effect (GLMM: treatment: $F_{1,41..0} = 3.817$, $P = 0.060$; helper size: $F_{1,41·0} = 0.517$, $P = 0.478$; treat*helper size $F_{1,41·0} = 1.396$, $P = 0.247$; Table 2). The amount of plankton feeding correlated negatively with the helping effort of large and small helpers in the plankton reduction treatment (Pearson correlation: $r_s = -0.411$, $n = 32$, $P = 0.020$), but not so in the control treatment (Pearson correlation: $r_s = -0.670$, $n = 32$, $P = 0.715$; Fig. 1). The amount of defence and digging did not differ between treatments. Overall, large helpers dug more than small helpers (see Table 2).

EGG PREDATOR AND SAND EXPOSURE

When confronted with an egg predator close to the breeding shelter, the fish in the plankton reduction treatment had a longer attack latency than the fish in the control treatment (t-test, $t_{31} = -2.241$, $P = 0.032$; Table 3). Moreover, in the plankton reduction treatment small helpers and juveniles showed less defence against the presented *T. vittatus* than in the control treatment (t-test, small helpers: $t_{31} = 2.166$, $P = 0.038$; juveniles: $t_{28} = 2.067$, $P = 0.048$; Fig. 2). This was not the case for large helpers (Mann–Whitney U-test, $z_{32} =$
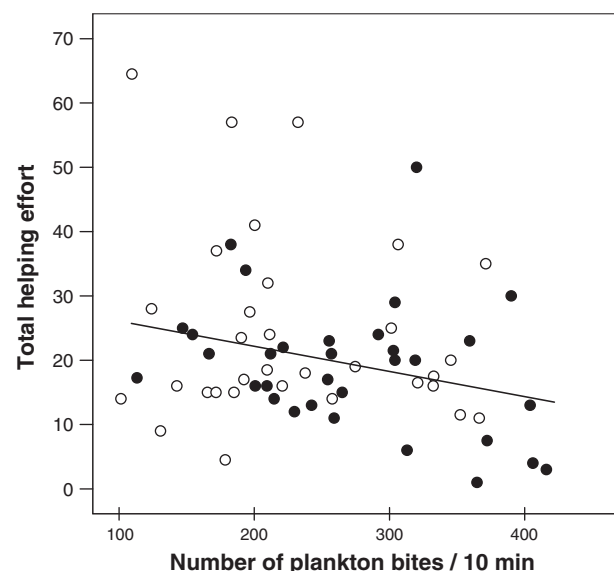

Fig. 1. Relationship between the total helping effort and the number of plankton bites per treatment. The control treatment is represented by open circles and the plankton reduction treatment by black circles. A regression line is fitted for the significant negative correlation in the plankton reduction treatment.

Table 3. Digging frequencies (left) and defence frequencies (right) from the sand and egg predator exposure trials for the plankton reduction and control treatments, and for both treatments combined

	Sand exposure		(# of digging)		Egg predator exposure		(# of defence)	
	Control mean ± SE	Plankton mean ± SE	Test statistic	P	Control mean ± SE	Plankton mean ± SE	Test statistic	P
Latency	147·1 ± 22·7	134·7 ± 19·9	† t_{13} = 0·411	0·648	68·3 ± 12·6	108·4 ± 12·7	† t_{33} = −2·241	**0·032**
BM	2·0 ± 0·9	4·3 ± 1·6	U_{32} = 93·50	0·196	1·3 ± 0·5	0·5 ± 0·2	U_{33} = 114·00	0·406
BF	11·0 ± 2·4	13·0 ± 3·4	† t_{31} = −0·202	0·841	1·8 ± 0·6	4·6 ± 1·5	† t_{33} = −1·453	0·156
LH	8·1 ± 2·7	6·4 ± 2·2	† t_{31} = 0·485	0·631	2·2 ± 0·6	2·3 ± 1·3	U_{33} = 113·00	0·400
SH	2·9 ± 0·9	2·1 ± 0·5	† t_{31} = 0·732	0·470	6·9 ± 2·1	3·2 ± 1·1	† t_{33} = 2·067	**0·038**
JUV	1·5 ± 0·8	0·3 ± 0·1	U_{29} = 92·50	0·591	8·0 ± 3·3	1·7 ± 0·7	† t_{30} = 2·124	**0·048**
	Treatments combined				Treatments combined			
	mean ± SE	mean ± SE			mean ± SE	mean ± SE		
LH vs. SH	7·3 ± 1·7	2·5 ± 0·5	‡ t_{32} = 3·295	**0·002**	2·3 ± 0·7	5·2 ± 1·3	‡ t_{29} = −2·928	**0·007**
LH vs. BM	7·3 ± 1·7	3·1 ± 0·9	z_{31} = −2·348	**0·019**	2·3 ± 0·7	0·9 ± 0·3	z_{32} = −1·816	<u>0·069</u>

We used *t*-tests († = independent sample *t*-test; ‡ = paired sample *t*-test), Mann–Whitney *U*-tests (for unpaired data, test statistic: *U*) and Wilcoxon signed-ranks tests (for paired data, test statistic: *z*). BM, breeder males; BF, breeder females; LH, large helpers; SH, small helpers; JUV, juveniles. Significant *P*-values are highlighted in bold; the underlined *P*-value is between 0·05 and 0·10.

−0·842, *P* = 0·423; Fig. 2). Overall, juveniles and small helpers showed the highest defence frequencies against the presented egg predators, followed by female breeders, large helpers, and male breeders (Table 3).
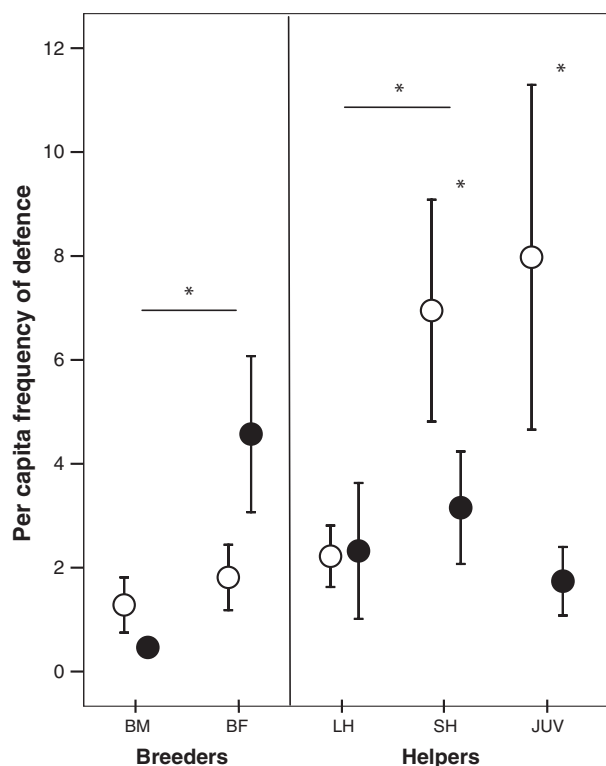

Fig. 2. Per capita frequency of defence for all types of group members in the control treatment (open circles) and in the plankton reduction treatment (black circles) against experimentally exposed egg predators. BM: breeder males, BF: breeder females, LH: large helpers, SH: small helpers, JUV: juveniles. Means ± SE are shown, * denotes *P* < 0·05.

There were no treatment effects on digging latency and total amount of digging in the sand exposure trials. When potential treatment effects were not considered, a similar digging pattern was seen in the sand exposure trials as in the focal observations; large helpers dug more than small helpers (paired *t*-test: t_{32} = 3·295, *P* = 0·002). We found that the breeder females dug most, followed by large helpers, male breeders, small helpers, and juveniles (Table 3).

HELPER SPACING AND DISPERSAL

In the plankton reduction treatment both large and small helpers increased the average distance from the breeding shelter and overall, large helpers went further away from the breeding shelter than small helpers, but there was no interaction effect between treatment and helper size (GLMM: treatment: $F_{1,30·0}$ = 17·10, *P* < 0·001; helper size: $F_{1,30·0}$ = 35·71, *P* < 0·001; treatment × helper size: $F_{1,30·0}$ = 0·30, *P* = 0·585; Fig. 3a). The same pattern emerged regarding average height in the water column (GLMM: treatment: $F_{1,29·2}$ = 16·29, *P* < 0·001: helper size: $F_{1,30·4}$ = 48·40, *P* < 0·001; treatment × helper size: $F_{1,30·1}$ = 0·99, *P* = 0·329; Fig. 3b). The treatment did not influence the time inside the breeding shelter, but overall small helpers spent more time in the breeding shelter than large helpers (GLMM: treatment: $F_{1,26·8}$ = 1·00, *P* = 0·326; helper size: $F_{1,27·1}$ = 8·41, *P* = 0·007; treatment × helper size: $F_{1,27·1}$ = 0·60, *P* = 0·444; Fig. 3c). No helper dispersal was observed in either treatment, although some individuals repeatedly explored the dispersal shelter, especially in the first week of the experiment.

Discussion

Our results show that global food reduction in cooperatively breeding fish caused helpers to roam further and increase
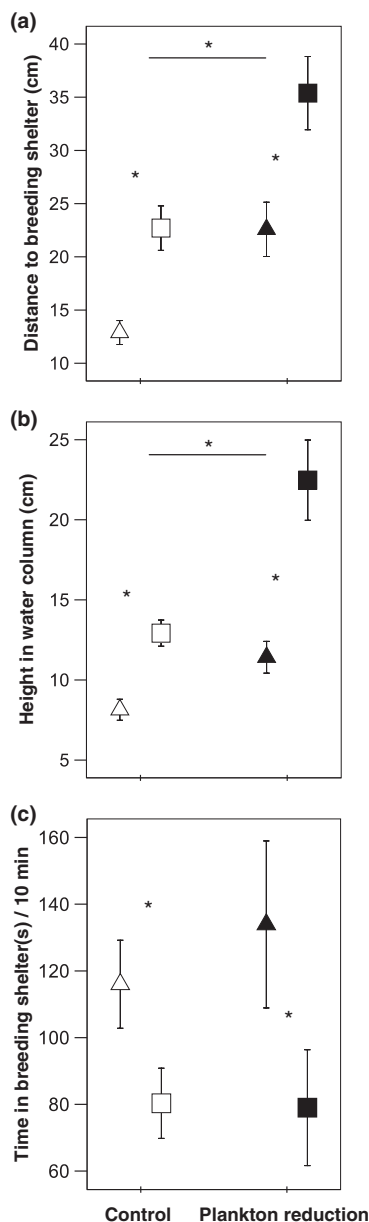
Fig. 3. Helping spacing behaviour in dependence of treatment (control treatment: open characters; plankton reduction treatment: black characters) and helper size (small helpers: triangles; large helpers: squares). The top graph (a) shows the mean distance to shelter, the middle graph (b) the mean height in the water column and the bottom graph (c) the mean time spent in the breeding shelter. Means ± s.e. are shown, *denotes P < 0.05.

their feeding effort. Moreover, in the reduced food condition all group members increased their attack latency on experimentally presented egg predators, and small sized helpers decreased the defence effort against them.

OPPORTUNITY COSTS OF IMPAIRED RESOURCE ACQUISITION

By using plankton nets we roughly halved the food availability to group members. As predicted, small and large sized helpers consequently increased their feeding effort compared

with the unimpeded controls. This significantly affected the spacing pattern of helpers, as apparently they had to roam further and higher up in the water column to fulfil their nutritional needs in the plankton reduction treatment. *N. pulcher* do not compete for food when feeding on plankton in the water column; they do not feed very close to each other as differently sized fish feed at different heights (Gashagaza 1988), and plankton is virtually non-depreciable. Helpers did not switch from plankton to benthos feeding when less plankton was available. However, there was a significant negative relationship between the number of plankton and benthos bites in the plankton reduction treatment only, suggesting a trade-offs between these two types of feeding when less of the preferred plankton is available. This is probably the reason why small helpers performed even less benthos bites in the plankton reduction treatment than in the control situation. Interestingly, helpers seemed to increase plankton feeding rates when conditions deviated from average in both directions, when plankton availability was very good or when it was strongly reduced: as outlined, the plankton feeding rate in the plankton reduction treatment exceeded that of the control treatment reflecting the increased demand, but within the control treatment there was a positive correlation between the number of invertebrates found in the plankton tows and the number of plankton bites performed.

DISPERSAL

In *N. pulcher* territory quality is not affected by the zooplankton supply in the water column as food is mainly consumed outside of the territory boundaries. Therefore, as predicted, there was no treatment effect by this experiment on subordinate dispersal. This contrasts with results of a study where another ecological constraint – mortality risk – was experimentally varied in the same population using a similar set-up; in that experiment, reduced predation threat raised the propensity of helpers to disperse (Heg *et al.* 2004), which met the prediction because the incentive to stay in the home territory to gain safety benefits was reduced (Taborsky 1984).

Two other studies have applied food reduction in cooperative breeders. Local food reduction within territories of western bluebirds (*Sialia mexicana*) caused increased dispersal of group members, suggesting an important role of 'resource wealth' of the home territory for delayed dispersal (Dickinson & McGowan 2005). Food reduction within colonies of the termite *Cryptotermes secundus* also increased the dispersal tendencies as predicted (Korb & Schmidinger 2004). These two studies had manipulated food as a crucial resource locally, i.e. within the home territory of the test animals, which contrasts with our food manipulation on a global scale. When another pivotal resource – the number of shelters – was experimentally reduced within *N. pulcher* territories, the number of helpers also declined, pointing towards a similar constraint-based decision as in the local food reduction experiments in bluebirds and termites (Balshine *et al.* 2001).

Other experiments testing for the significance of ecological constraints for dispersal decisions *improved* resource

availability, thereby reducing the costs of resource acquisition instead of increasing them. Either food was augmented in the home territories of subordinates (prairie voles, *Microtus ochrogaster*: Cochran & Solomon 2000; Lin *et al.* 2006; sociable weavers, *Philetairus socius*: Covas, Doutrelant & du Plessis 2004; carrion crows, *C. corone corone*: Baglione *et al.* 2006; Mongolian gerbils, *Meriones unguiculatus*: Liu *et al.* 2009), or breeding shelters were augmented in their neighbourhood (green woodhoopoes, *Phoeniculus purpureus*: Du Plessis 1992; red-cockaded woodpeckers, *Picoides borealis*: Walters, Copeyon & Carter 1992; *N. pulcher*: Bergmüller, Heg & Taborsky 2005a). Except in gerbils, these manipulations showed the expected effects on dispersal propensity and group structure, supporting the hypothesis that subordinates base their decision to stay or leave on the costs of resource acquisition and the potential to breed independently. In contrast, our study suggests that if critical resources such as food are used mainly outside of the territories, even drastic changes like reducing the food by half do not alter the pay-off relations between staying in a group and dispersing, hence dispersal propensity is not affected. This highlights the importance of the spatial distribution of critical resources (availability within or outside a territory or colony) on dispersal decisions of subordinate group members.

EFFECTS OF RESOURCE ACQUISITION COSTS ON HELPING AND OTHER BEHAVIOURS

When helpers move further away from the shelter and stay longer high up in the water column because of reduced food availability they have to bear two consequences. Firstly, this increases the risk of predation. Field experiments showed that *N. pulcher* helpers move closer to shelter to increase their survival probability when predation risk is high (Heg *et al.* 2004). This suggests a trade-off between foraging and safety when food is limited. Secondly, when helpers move further away from the territory they may be constrained to show helping behaviour, e.g. territory defence, territory maintenance and brood care. Consistent with this expectation, we found (i) a marginal decline in total helping effort when plankton availability was reduced and the helpers had to roam further to feed, and (ii) a negative correlation between plankton feeding and helping effort in the plankton reduction treatment. Apart from the mere limitation because of opportunity costs, reducing cooperation might be a strategic decision as helping is energetically costly (Grantner & Taborsky 1998; Taborsky & Grantner 1998).

We did not find a treatment effect on territory maintenance, but overall, large helpers performed more digging than small helpers, which is in accordance with previous studies (Balshine-Earn *et al.* 1998; Bruintjes & Taborsky 2008) and confirms size-related task differentiation in this species. Small helpers were less exposed to aggression by dominants in the plankton reduction treatment, which probably reflects reduced opportunities for group members to interact with each other when roaming further away from the territory to feed.

Our prediction that increased opportunity costs would cause reduced helping levels was confirmed also when egg predators were experimentally presented. In the food reduction treatment, group members attacked egg predators later, and small helpers and juveniles showed generally less defence against them in this condition than when food was not constrained. This confirms our prediction that an effect of food limitation and opportunity costs should be particularly strong in small (i.e., immature) group members, as these dispose of lower body reserves. In the functional context, this is all the more remarkable because small group members stay usually closest to the breeding shelter, thereby guarding the most vulnerable offspring stages (Heg *et al.* 2004; R. Bruintjes & M. Taborsky, unpublished data). This result is also consistent with the detrimental effect of an experimental reduction of helper numbers on the survival of small guarded offspring (Brouwer, Heg & Taborsky 2005).

Similar to our results, experimental food reduction in the termite *C. secundus* also caused an increase in self maintenance (feeding) at the expense of cooperative behaviour (trophallaxis). In studies where the costs of resource acquisition were *reduced* by food augmentation on the home territory, the response of subordinate group members was somewhat divergent. In most studies of birds and in a study of meerkats the extra food promoted helping effort (see the Introduction section for references), whereas in social weavers (*P. socius*) it caused increased dispersal and reduced helping levels (Covas, Doutrelant & du Plessis 2004). This reveals that clear predictions about effects of experimental variation of resource acquisition costs on helping can be difficult to make if resources are augmented on a local scale, which usually affects the decision to stay or disperse as well.

In conclusion, our study shows that helping effort can depend on a trade-off between resource acquisition and cooperative behaviour, which highlights the importance of resource acquisition costs as an ecological constraint determining helping levels in cooperative breeders. By varying the global food availability our experimental approach did not change the resource distribution between territories and hence no incentive was given for subordinate group members to disperse, which might have interfered with decisions about helping behaviour (cf. Bergmüller, Heg & Taborsky 2005a). Thereby this experiment revealed that, even if dispersal decisions are not affected, the costs of resource acquisition can be an important predictor of foraging, spacing and helping behaviour in highly social vertebrates.

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Supporting Information

Additional Supporting information may be found in the online version of this article.

Appendix S1. Size classes and taxa of invertebrates from plankton tows.

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