



Size-dependent task specialization in a cooperative cichlid in response to experimental variation of demand

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Many social species show some form of task specialization among group members. In cooperative vertebrates, this usually does not coincide with morphological differentiation. In species with indeterminate growth, however, size differences between subordinates may promote task specialization in the performance of helping behaviours, depending on size-specific capabilities, opportunities and cost/benefit ratios. In the cooperatively breeding cichlid fish *Neolamprologus pulcher*, helpers perform different helping tasks. To examine the effects of helper size, which reflects age, on cooperative behaviour in the field, we experimentally presented egg predators that do not threaten helper survival. In the egg predator treatment, large and small helpers increased defence and all helpers roamed further from the breeding shelter, presumably to keep potential egg predators at a safe distance from the brood. Additionally, small helpers defended more against egg predators presented close to the breeding shelter than large helpers, whereas the latter put more effort into digging experimentally added sand out of the breeding shelter. Our results show size(age)-specific task specialization of helpers in a cooperatively breeding vertebrate, which is reminiscent of eusocial insects.

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Many social species show some kind of division of labour, for example, honeybees, *Apis mellifera* (Ribbands 1952), termites (Bartz 1979), ants (Hölldobler & Wilson 1990), naked mole-rats, *Heterocephalus glaber* (Lacey & Sherman 1991) and meerkats, *Suricata suricatta* (Clutton-Brock et al. 2004). In invertebrates, this specialization is often associated with morphological differentiation (e.g. in ants: Wilson 1971; Hölldobler & Wilson 1990; Bourke & Franks 1995). Division of labour in social insects has been shown among morphologically identical individuals as well (Oster & Wilson 1978). This temporal polyethism, the change in behaviour that occurs as an individual ages, has been observed in a number of social insect species in which older individuals tend to take on more life-threatening tasks (e.g. Gerber et al. 1988; Bourke & Franks 1995).

In cooperatively breeding vertebrates, subordinates delay dispersal and help to raise offspring of dominants before starting to

reproduce independently. Unlike in most eusocial insects, subordinates of cooperatively breeding vertebrates are usually morphologically similar to breeders, with the exception of naked mole-rats (O'Riain et al. 2000) and meerkats (Russell et al. 2004), in which reproductive females are bigger and older than subordinates, and cooperative fishes, where size and age differences between dominant and subordinate group members may occur in either sex (Taborsky & Limberger 1981; Taborsky 1987; Martin & Taborsky 1997; Kohler 1998; Heg et al. 2005; reviewed in Taborsky 2009). Although the division of labour between subordinate and dominant individuals has been well documented in some cooperatively breeding fishes, birds and mammals (e.g. Taborsky 1987; Lacey & Sherman 1991; Martin & Taborsky 1997; Clutton-Brock et al. 2004; Gilchrist & Russell 2007; Kitchen & Beehner 2007; Desjardins et al. 2008; Pacheco et al. 2008; Ridley & Raihani 2008), much less is known about task specialization between helpers in vertebrates (Taborsky & Limberger 1981; Taborsky et al. 1986; Heinsohn & Cockburn 1994; Clutton-Brock et al. 2000, 2003; Arnold et al. 2005). The substantial size variation among brood care helpers in many group-breeding vertebrates might predispose certain helpers to perform specific helping behaviours, since

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helpers often participate in very different tasks ranging from direct brood care to guarding, territory maintenance and defence (Taborsky & Limberger 1981; Taborsky et al. 1986; Heinsohn & Cockburn 1994; Clutton-Brock et al. 2003; Komdeur 2006). This applies particularly in taxa with indeterminate growth such as fishes, where body size is not fixed but subject to a steady change, providing potential for a size-dependent, temporal behavioural specialization or polyethism.

Neolamprologus pulcher is a cooperatively breeding cichlid fish endemic to Lake Tanganyika, Africa. In this species, helpers defend the territory against conspecific and heterospecific space competitors and predators of eggs, larvae, young and adults; they perform territory maintenance mainly by digging sand away from the shelters used for hiding and breeding, and they care for the brood by cleaning eggs and larvae with their mouth and by fanning (Taborsky & Limberger 1981; Taborsky 1984). Performing helping behaviour is costly in terms of energy expenditure (Grantner & Taborsky 1998; Taborsky & Grantner 1998), which reduces the helpers' growth rate (Taborsky 1984; Heg et al. 2004b; Bergmüller et al. 2005a). Breeders benefit from their helpers by an increased survival of offspring and a reduced workload in relation to helper number (Balshine-Earn et al. 1998; Brouwer et al. 2005), which increases fecundity (Taborsky 1984) and affects egg size (Taborsky et al. 2007). Experimental evidence suggests that pay to stay is an important mechanism for subordinate helping behaviour in *N. pulcher* (Taborsky 1984, 1985; Balshine-Earn et al. 1998; Bergmüller & Taborsky 2005; Bergmüller et al. 2005a; Stiver et al. 2005; Bruintjes & Taborsky 2008).

In the field, we investigated the effects of helper size (which reflects age; Skubic et al. 2004) on subordinate helping behaviour by exposing half of the experimental groups to the opportunistic egg predator *Telmatochromis vittatus*. The latter are about the same size as helpers, are not resource competitors and are no threat to helper survival. Additionally, we temporarily presented egg predators close to the breeding shelter or covered the shelters with sand to increase the need for help experimentally. We predicted that helpers would increase their defence effort if egg predators were added and increase digging if shelters were partly filled with sand. Furthermore, we predicted that helpers of different sizes would specialize in divergent tasks, depending on capability, opportunity and efficiency. For instance, small helpers should be better suited to defend the brood against egg predators, since they usually stay closer to the breeding shelter because of their greater vulnerability to predators than large helpers (Heg et al. 2004a). In contrast, large helpers should rather specialize in digging, since large individuals would be more efficient at taking up and carrying sand with the mouth than small ones. Beyond this it is difficult to make detailed predictions about optimal task specialization, however, because the effects of different capabilities, opportunities and efficiency might interact and neutralize or counter one another. In addition, relatedness and incentives to pay for staying differ between small (young) and large (older) helpers, because relatedness between helpers and beneficiaries declines with helper age (Taborsky & Limberger 1981; Dierkes et al. 2005), whereas the costs imposed on dominants by helpers increase with their size (Taborsky 1985), mainly because of reproductive competition (Dierkes et al. 1999; Heg et al. 2006; Heg & Hamilton 2008; Mitchell et al. 2009).

METHODS

Study Species and Egg Predators

Neolamprologus pulcher is a common cooperatively breeding cichlid occurring all around the shores of Lake Tanganyika (Duftner et al. 2007). The fish were studied by SCUBA diving at the southern

tip of the lake at Kasakalawe point near Mpulungu, Zambia, from September to November 2005. Groups are composed of a dominant pair with up to 14 helpers of different sexes and size classes, including immature and mature individuals (Taborsky & Limberger 1981; Balshine et al. 2001). Maturity is reached at about 35 mm standard length (SL; Taborsky 1985), and in our study population female breeders are on average 52 mm SL and male breeders 60 mm SL (Balshine et al. 2001). Territories at our study site are composed of distinct patches of stones that are used as breeding and hiding shelters (Balshine et al. 2001; Heg et al. 2008). Shelters are created and maintained by digging away sand and debris from underneath stones. Our breeding colony consisted of several hundred territorial groups. Group territories were marked with numbered stones and mapped, and group composition was determined by repeated focal observations.

We used an unspecialized egg predator species, *T. vittatus*, to measure helper defence and task specialization. To assess the average natural density of *T. vittatus* in our study colony, we performed two types of survey: (1) area survey: the study area was marked with sisal lines in 100 squares of 4 m² each, which were checked for the presence and number of *T. vittatus*; (2) line transect survey: a measuring line 70 m long was placed straight through the study area, and after waiting 1 day, we noted the abundance and size (SL estimate in mm) of all *T. vittatus* within 20 cm on both sides of the line, together with the percentage of rock coverage; for analysis, the total distance was partitioned into 35 sections each of 2 m. Both surveys were performed once. Rock coverage was measured because it has been suggested that *T. vittatus* shows a preference for rocky habitats (Konings 1998), which corresponds to the preferred habitat of *N. pulcher* (Heg et al. 2008).

Experimental Set-up

Experimental units were created as follows. Two to three nearby group territories, 1–1.5 m from each other, were selected haphazardly. Each unit consisted of at least two group territories and each group consisted minimally of a breeder male (BM), a breeder female (BF), one large helper (LH >35 mm SL) and one small helper (SH; 25–35 mm SL). Furthermore, 25 of the 32 groups possessed juveniles (JUV: 15–24.5 mm SL). BM had a mean size \pm SD of 56.3 ± 3.7 mm SL, range 48.0–62.0 mm, and BF measured 49.9 ± 3.4 mm SL, range 42.0–57.5 mm. On average, groups consisted of 1.5 ± 1.2 LH, 1.8 ± 0.8 SH and 1.9 ± 1.7 JUV. We selected groups with differently sized helpers, because helpers of dissimilar sizes react differently to high perceived intruder pressure (Bruintjes & Taborsky 2008). As described above, maturity is reached at about 35 mm SL, which could change their behavioural strategies (Skubic et al. 2004). We placed a cage (2 \times 2 \times 2 m; aluminium frame covered with a sturdy plastic net, mesh size 2.5 \times 2.5 mm to allow free plankton flow) over each group territory as described by Heg et al. (2004a).

Per trial ($N=8$), two cages were placed close to each other (1–6 m apart) to minimize 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 in the other cage we put 22 *T. vittatus* ($N_{\text{total}}=16$ cages, including 33 groups in total; two groups per cage were used for focal observations, making 32 focal observation groups; see below for observation details). The egg predators had a mean SL of 33.7 ± 5.4 mm. The egg predator density created by this treatment ($22/4=5.5$ individuals/m²) represents a moderately high *T. vittatus* density in this colony (see Results).

The cages contained the entire environment the focal group members would normally use, and the fish community present at the respective places when the cages were established, excluding

all piscivores. One to three *N. pulcher* per experimental group were caught in transparent tubes and hand nets to be sexed, measured (SL to 0.5 mm) and fin clipped. We clipped fins by carefully excising half of a single fin ray of the dorsal fin to facilitate helper identification. To minimize disturbance, only similar-sized group members were caught and marked. The identification and the size estimation of other individuals were facilitated by comparing their sizes with those of measured and fin-clipped group members and by placing a marked measuring line into the territory. At two opposite cage sides a door (60 × 80 cm) inserted 35 cm from the ground could be opened with zippers for conducting behavioural observations. Each trial lasted 2 weeks.

Behavioural Observations

The fish in the control and egg predator cages behaved normally and showed no signs of stress as revealed by comparison with conspecifics outside the cages; for example the feeding rates were similar (200–400 plankton bites per 15 min, Balshine-Earn et al. 1998; Heg et al. 2004a; Brintjes et al. 2010). Before the start of each replicate, one small and one large helper per group were observed once for 10 min each and their behaviour was recorded for baseline behaviour data. During the experiment, one small and one large helper of two groups per cage were observed in random order three times for 10 min each. In total, helpers of 32 territorial groups were observed between 0830 and 1700 hours producing 190 focal observations (two recordings were lost). All observed behaviour was recorded in frequencies, with the exception of time spent inside the breeding shelter. The behavioural observations were recorded on plastic slates by three observers.

The recorded behaviours included overt attacks (ramming, biting, mouth fighting), restrained aggressive displays (frontal approach, head-down display, S-shaped bending, head jerking, opercula spreading, dorsal fin raising), submissive behaviour (tail quivering, hook display, fleeing), territory maintenance (digging, i.e. carrying away sand with the mouth) and feeding (plankton or benthos bites; for description of behaviours see Taborsky 1984).

Sand Addition and Egg Predator Presentation Trials

To get a standardized estimate of helping propensity, each experimental group was exposed twice to sand addition and egg predator presentation trials. Both trials were performed once in the first and once in the second week of the experiment in random order. In the sand addition trials, we carefully covered the breeding shelter by steadily pouring approximately 0.25 litres of sand in the entrance to induce digging (this simulates natural conditions created by water movements after a heavy surge, which is a source of mortality for small offspring; Taborsky & Limberger 1981). The 10 min recording of digging frequencies started after the first individual of the group began to dig, or after 5 min when no digging was shown until then. We recorded latency to first digging (continuously monitored from the end of the manipulation), by which group member it was performed (BM, BF, LH, SH or JUV), and all individual digging frequencies. Digging behaviour was analysed per capita per group member type.

In the predator presentation trials a *T. vittatus* (mean SL ± SE = 32.9 ± 2.3 mm, *N* = 17 individuals), was presented for 10 min in a clear Plexiglas tube (length: 15 cm; inner diameter: 8.2 cm) at 5 cm from the main breeding shelter entrance. We recorded the latency to first attack or aggressive display, by which group member it was performed, all overt and restrained aggression against the egg predator, and the activity level of the exposed egg predator on a scale of 0–5 (activity level 0 means the *T. vittatus* showed no movements during the entire presentation; activity

level 5 means the egg predator was in motion during the entire presentation). There were no differences in the size of the egg predators and in their activity between the two treatments (size: *t* test: $t_{48} = 0.146$, $P = 0.885$; activity: Mann–Whitney *U* test: $Z = -0.535$, $N_1 = N_2 = 32$, $P = 0.593$).

Helper Spacing and Dispersal

To determine individual helper spacing, during each focal observation, we estimated once every minute the focal helper's height in the water column as well as its distance from the breeding shelter (in cm). Additionally, the frequency of breeding shelter visits and the total time inside the breeding shelter were recorded. 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, 0.5–1.5 m from the group territories. The shelters were provided to test whether helpers would disperse and breed independently contingent on the presence of egg/larvae predators, because it has been shown in the same study population that predation risk for larger group members is an ecological constraint for subordinate dispersal (Heg et al. 2004a). Furthermore, previous studies have shown that *N. pulcher* preferentially disperse to neighbouring territories (Stiver et al. 2004; Bergmüller et al. 2005b; Heg et al. 2008). The dispersal shelters were checked for occupancy once a week during 20 min observations. Individuals were considered to have dispersed if they permanently occupied and defended the dispersal shelter (Heg et al. 2004a).

Ethical Note

The large cages used for this experiment did not hinder *N. pulcher* in their movements, since the cages were sufficiently large to encompass the natural territory area and group members' home ranges (median territory size 0.315 m², range 0.078–1.010 m²; Balshine et al. 2001). Although *N. pulcher* mainly feeds on zooplankton outside of their home territory (Taborsky & Limberger 1981; Gashagaza & Nagoshi 1986), the fish usually do not feed higher in the water column than 1 m (Gashagaza 1988; Brintjes et al. 2010). Furthermore, the *T. vittatus* used were too small to be a threat to the helpers, including fry and juveniles; juveniles were frequently seen attacking the egg predators (see Results), which suggests very low threat levels of the egg predators for juveniles.

The *T. vittatus* used as egg predators were attacked by *N. pulcher* group members with similar intensity and frequency as in the natural situation outside of the cages, and they showed normal behaviour including foraging, exploration and social interactions. All fish used in the experiments were monitored at least at intervals of 3–5 days to ascertain their wellbeing. The *T. vittatus* used for the egg predator presentation trials were used for a maximum of 40 min and released directly thereafter.

Some *N. pulcher* individuals were fin-clipped for identification purposes. Only half of a single fin ray was clipped from the dorsal fin. The marked fish behaved normally and the fin rays regrew within 1–2 months (personal observation). At the end of each trial the cage was simply raised and removed from the location, leaving the fish undisturbed and exactly where they had been before the experiment.

Data Analyses

Normality of data distributions was checked with the one-sample Kolmogorov–Smirnov test and all data were tested for homogeneity of variance. Means were taken of all focal behavioural data and, if necessary, the data were transformed using logarithmic or square-root transformations. For normally distributed data we used general linear mixed models (GLMM) with fixed effects:

treatment, helper size and treatment*size; random effects: cage, group nested in cage and observer; covariates: time of observation, date and group size (number of fish present in the group >25 mm SL; juveniles were excluded because of their relatively little effect and highly varying numbers). Nonsignificant (interaction) effects, nonsignificant covariates and redundancies ($P > 0.250$) were discarded from the statistical model. Nevertheless, treatment, helper size and the interaction effect treatment*helper size always remained in the model. Treatment*helper size is only presented here if $P < 0.250$.

Combined effects, without taking the treatment into account, were analysed with paired t tests when the data were normally distributed. When the above-mentioned transformations did not generate normal distributions we used Wilcoxon signed-ranks tests. Only two-tailed tests were performed.

Correlations were calculated with Pearson correlation analysis for normally distributed data with homogeneous variances; otherwise we used the Spearman rank correlation analysis. Multiply tested data were controlled for false discovery rates (Verhoeven et al. 2005). All statistical analyses were performed using SPSS 13.0 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Natural Density of Egg Predators

The area surveys showed a mean density of 1.45 egg predators/ m^2 in the study colony (range 0–9 individuals/ m^2). The egg predators had a mean SL of 31.0 ± 0.3 mm ($N = 100$ survey squares). The line transects ($N = 35$ survey rectangles) revealed a mean density of 2.13 *T. vittatus*/ m^2 (range 0–13 individuals/ m^2). The density estimates obtained by these two methods did not differ significantly from each other (Mann–Whitney U test: $Z = -0.264$, $N_1 = 100$, $N_2 = 35$, $P = 0.792$). The line transect revealed a positive correlation between the number of *T. vittatus* and the percentage of rock coverage (Spearman rank correlation: $r_s = 0.587$, $N = 35$, $P < 0.001$), suggesting that *T. vittatus* and *N. pulcher* prefer living in similar rocky habitat and interact because of this.

Helping Behaviour

In the egg predator treatment, both large and small helpers performed more defence behaviour than in the control treatment, and there was no difference between the two helper size categories (GLMM: treatment: $F_{1,29,2} = 12.00$, $P = 0.002$; helper size: $F_{1,29,5} = 0.54$, $P = 0.468$). Defence solely against *T. vittatus* was higher in the egg predator treatment than in the control treatment (Mann–Whitney U test: $Z = -4.86$, $N_1 = N_2 = 32$, $P < 0.001$). When defence was analysed excluding aggressive behaviour against *T. vittatus*, no significant treatment and helper size differences were found (Table 1). Digging behaviour did not differ significantly between the treatments, but independently of the treatment, large helpers tended to perform more digging than small helpers (Table 1).

Sand Addition and Egg Predator Presentation Trials

The total group digging activity in the sand addition trials was higher in the egg predator treatment than in the control treatment (t test: $t_{32} = -2.686$, $P = 0.011$). No significant treatment differences were detected within different categories of group members (BM, BF, LH, SH and JUV), but there was a tendency for breeder males and breeder females to perform more digging behaviour in the egg predator treatment than in the control (Fig. 1, Table 2). Independently of the treatment, large helpers dug significantly more often than small helpers, and breeder females performed

Table 1
Comparison of behaviour in relation to treatment and helper size

	Treatment		Helper size	
	Z	P	Z	P
All defence (not against <i>T. vittatus</i>)	-0.334	0.738	-1.598	0.110
Digging	-0.472	0.637	-1.903	0.057
Submissive behaviour	-0.323	0.747	-2.028	0.043
Received submissive behaviour	-0.039	0.969	-0.997	0.319
Aggression (among group members)	-0.206	0.837	-0.521	0.602
Received aggression (from group members)	-0.259	0.795	-0.098	0.922

Differences between the control and egg predator treatments were tested with the Wilcoxon signed-ranks test ($N = 32$). Helper size effects were checked with the Mann–Whitney U test ($N = 64$). Bold indicates a significant P value and italics $P < 0.1$.

more digging than breeder males (Table 3). No treatment difference was observed in the latency to first digging after the sand addition (Table 2).

In the egg predator presentation trials, no treatment differences were found in the amount of defence for any category of group members (Fig. 2, Table 2). However, small helpers defended significantly more often against the egg predator than large helpers, and female breeders performed more defence against the egg predator than male breeders when both treatments were combined (Fig. 2, Table 3).

Social Behaviour

No treatment differences were detected between received and performed aggressive and submissive behaviours among members of the same group (Table 1). When we combined all data, large helpers performed less submissive behaviour than small helpers (Table 1).

Helper Spacing and Dispersal

All helpers (small and large) tended to move further away from the breeding shelter in the egg predator treatment than in the control (GLMM: treatment: $F_{1,28,3} = 3.18$, $P = 0.085$; Fig. 3a).

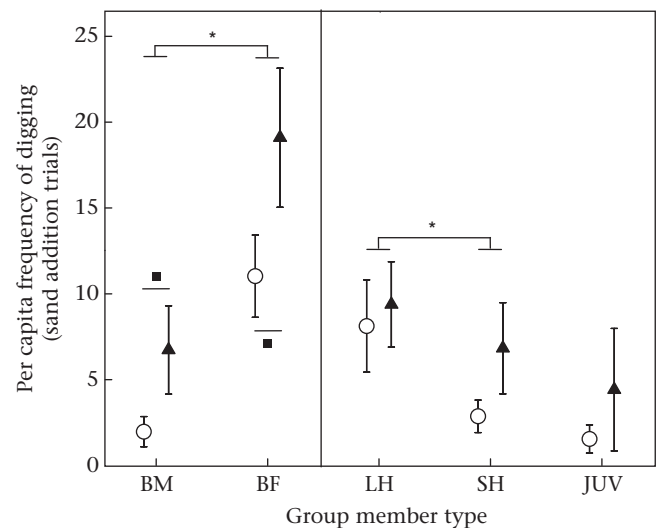


Figure 1. Per capita frequency of digging in the sand addition trials by all group member types in the egg predator treatment (black triangles) and in the control treatment (open circles). BM: breeder males; BF: breeder females; LH: large helpers; SH: small helpers; JUV: juveniles. Means \pm SE are depicted. * $P < 0.05$; ■ $P < 0.10$.

Table 2

Results from the sand addition and egg predator presentation trials for the egg predator and control treatments

	Sand addition		Test statistic	<i>P</i>	Egg predator presentation		Test statistic	<i>P</i>
	Control	Egg predator treatment			Control	Egg predator treatment		
Latency (s)	142.7±19.8	138.9±23.1	$t_{32}=0.128$	0.899	4.0±0.2	3.8±0.2	$t_{32}=0.734$	0.468
Frequency								
BM	2.0±0.9	6.7±2.6	$Z_{32}=-1.904$	0.057	1.2±0.5	0.6±0.3	$Z_{33}=-1.226$	0.220
BF	11.0±2.4	19.1±4.1	$t_{32}=-1.715$	0.096	2.4±0.7	7.0±4.0	$t_{32}=-1.560$	0.129
LH	8.1±2.7	9.4±2.5	$t_{31}=-0.651$	0.520	2.4±0.6	8.1±6.0	$Z_{34}=-0.262$	0.793
SH	2.9±0.9	6.8±2.7	$t_{31}=-1.405$	0.170	9.5±3.5	8.2±3.1	$t_{32}=0.248$	0.806
JUV	1.5±0.8	4.4±3.6	$Z_{28}=-0.526$	0.599	7.1±1.6	11.1±4.0	$t_{26}=-0.377$	0.710

Latencies to first occurrence and frequencies of digging sand (left side of the table) and defending against an egg predator (right side of the table) are shown (means ± SE). We used independent *t* tests (test statistic *t*) and Mann-Whitney *U* tests (test statistic *Z*). BM: breeder male; BF: breeder female; LH: large helper; SH: small helper; JUV: juvenile. Italics indicate *P* < 0.1.

Furthermore, the same GLMM showed that large helpers moved further away from the breeding shelter than small helpers, irrespective of the treatment (GLMM: helper size: $F_{1,29.9} = 45.12$, $P < 0.001$; Fig. 3a), and the covariate group size showed a significant effect (GLMM: group size: $F_{1,27.9} = 5.22$, $P = 0.030$) indicating that in larger groups the mean shelter distance of helpers was smaller than in small groups. No treatment effect was detected on the height of helpers in the water column, but large helpers moved significantly higher up in the water column than small helpers in both treatments (GLMM: treatment: $F_{1,29.0} = 1.84$, $P = 0.186$; helper size: $F_{1,29.5} = 40.00$, $P < 0.001$; Fig. 3b). In the egg predator treatment, helpers spent less time inside the breeding shelter than in the control situation, and for both treatments combined, small helpers spent more time in the breeding shelter than large helpers (GLMM: treatment: $F_{1,27.9} = 4.30$, $P = 0.048$; helper size: $F_{1,30.1} = 4.36$, $P = 0.045$; Fig. 3c).

No helper dispersal was observed in both treatments, although mainly in the first week of the experiment several individuals repeatedly explored the dispersal shelters.

Helper Foraging

The number of helper plankton bites was not affected by the treatment and no difference was detected between helpers of different sizes; however, the covariate 'group size' did have a significant negative effect: in large groups helpers performed fewer plankton bites than in small groups (GLMM treatment: $F_{1,13.0} = 1.98$, $P = 0.183$; helper size: $F_{1,30.1} = 1.15$, $P = 0.292$; group size: $F_{1,24.6} = 13.98$, $P = 0.001$). The treatment had no effect on the amount of benthos feeding, but small helpers tended to perform more benthos feeding bites than large helpers (GLMM: treatment: $F_{1,29.4} = 0.40$, $P = 0.843$; helper size: $F_{1,29.6} = 3.05$, $P = 0.091$), and only small helpers showed a significant negative correlation between the number of benthos and plankton bites (Pearson correlation: small helpers: $r_{30} = -0.478$, $P = 0.006$; large helpers: $r_{29} = 0.151$, $P = 0.417$). When the treatments were tested separately, a strong negative correlation between the number of plankton and benthos bites of small helpers was found only in the egg predator treatment (Pearson correlation: egg predator treatment: $r_{14} = -0.630$, $P = 0.009$; control: $r_{14} = -0.209$, $P = 0.437$).

Table 3

Results from the sand addition and egg predator presentation trials for the egg predator and control treatments combined

	LH	SH	LH vs SH Test statistic	<i>P</i>	BM	BF	BM vs BF Test statistic	<i>P</i>
Sand addition	8.7±1.8	4.9±1.5	$t_{33}=2.668$	0.012	4.3±1.4	15.5±2.5	$t_{32}=6.166$	<0.001
Egg predator presentation	5.2±3.0	8.8±2.3	$t_{33}=-2.618$	0.013	0.9±0.3	4.7±2.1	$Z_{33}=-3.410$	0.001

Large helpers (LH) are tested against small helpers (SH) and breeder males (BM) against breeder females (BF). We used paired sample *t* tests (*t*) and a Wilcoxon signed-ranks test (*Z*). Mean frequencies are shown ±SE. Bold indicates significant *P* values.

Offspring Production and Behaviour with and without Fry

Six groups produced fry in our experiment: three in the egg predator treatment and three in the control treatment. Behavioural data exist from five of the six groups with fry for the pre- and postfry situations; one group already had fry when the behavioural observations started. We checked for differences in defence, digging, spacing and plankton feeding between the periods before and after fry emerged. Only the number of plankton bites differed between these two periods. Both helper size classes showed fewer plankton bites in the postfry stage than in the pre-fry stage (Wilcoxon test: $Z = -2.090$, $N = 10$, $P = 0.037$).

DISCUSSION

Our field experiment revealed that group members adjust their defence and territory maintenance effort to increased demands. Furthermore, task specialization depended on body size and status of group members. Large helpers performed most of the digging behaviour in comparison to small helpers and, during the sand addition trials especially, large helpers and female breeders showed high digging performances. Defence behaviour of both small and large helpers was greater when the number of egg predators was experimentally increased, but small helpers in particular engaged in defence against egg predators when these were presented close to the breeding shelter, where they can be most harmful to a developing brood. In addition, juveniles frequently attacked the egg predators in this situation. The specialization of small group members in defence required close to the brood chamber probably reflects the greater opportunities of small fish to show this kind of help: as our results and previous studies have demonstrated (Gashagaza 1988; Bergmüller et al. 2005b; Brintjes & Taborsky 2008; Brintjes et al. 2010), they stay closer to the breeding shelter than large helpers, and average distance to this shelter determines helping frequencies (Werner et al. 2003).

Large helpers and breeder females performed low levels of defence against the egg predators, whereas breeder males almost never participated. This task differentiation appears to be efficient, because small helpers seem to defend the brood against the medium-sized egg predators used in our experiment as effectively

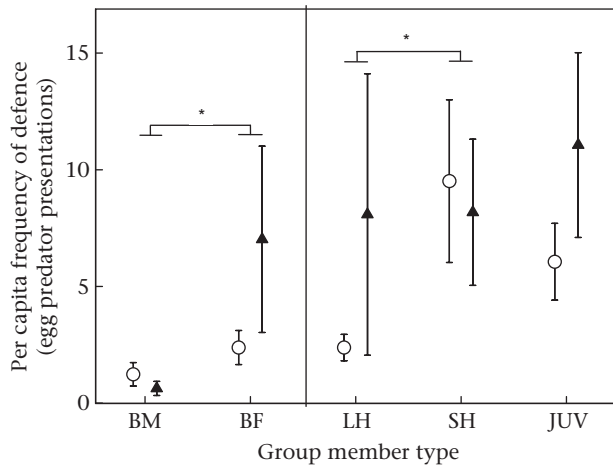


Figure 2. Per capita frequency of defence in the egg predator presentation trials by all group member types in the egg predator treatment (black triangles) and in the control treatment (open circles). Abbreviations and symbols as in Fig. 1.

as larger group members (R. Bruintjes, personal observation). Thus larger group members are somewhat exempted from this duty and can specialize in tasks where large body size is more important, such as removing sand from the breeding shelter (this study) or defence against large piscivore predators (Heg & Taborsky 2010). The task specialization of differently sized group members found in this study partly confirms results of an earlier laboratory study (Taborsky et al. 1986), which used a different, sequential presentation of predators, space competitors and conspecifics at different stages of the breeding cycle. That study had shown that breeders and helpers of *N. pulcher* to some extent specialize in attacking intruders of matching size, regardless of the species they belonged to. Furthermore it had shown that territory maintenance was mainly done by small group members while large intruders were threatening the group, which indicates behavioural flexibility and a specific response to the particular demands encountered by a group. This is also suggested by a field study involving presentations of predators of adults and young, and of breeder-sized conspecifics, in glass jars close to the breeding shelter, which revealed higher defence frequencies of female breeders than of any other type of group member against the presented predators and large female intruders. Only large male intruders were more often attacked by the male breeders (Desjardins et al. 2008).

Size-specific task specialization as shown by *N. pulcher* is reminiscent of the behavioural differentiation of insect castes that often diverge greatly in body size (Wheeler 1986; Hölldobler & Wilson 1990). However, several insect species also show temporal polyethism, in which individual specialization in behaviour changes with age, whereas the morphology remains constant (Oster & Wilson 1978; Kolmes 1985; Jeanne 1991; Robinson et al. 1994). For instance, in the ant species *Pheidole dentata*, just-hatched workers care for eggs and young larvae, young workers care for medium-sized larvae and older workers prefer nest work and foraging (Wilson 1976). Monomorphic insect species rarely divide tasks solely on the basis of size, but in the ant *Leptothorax longispinosus*, for example, there is a quantitative behavioural difference with large workers foraging more than smaller ones (Herbers & Cunningham 1983). This appears to have a similar functional background as task specialization in *N. pulcher*, in which larger individuals specialize in tasks that clearly benefit from large body size owing to increased efficiency. In *N. pulcher* the

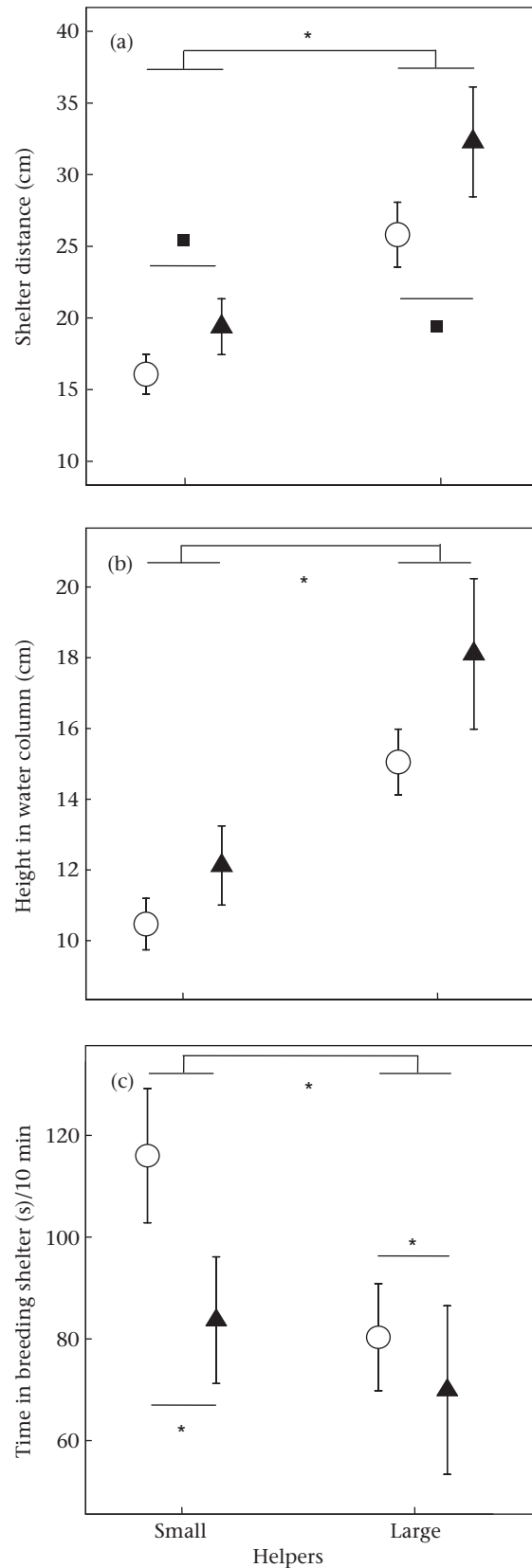


Figure 3. Spacing behaviour of small and large helpers in the egg predator treatment (black triangles) and in the control treatment (open circles). Depicted are the means \pm SE of (a) shelter distance, (b) height in the water column and (c) time inside the breeding shelter. * $P < 0.05$; ■ $P < 0.10$.

mechanisms underlying this task specialization are not yet known (cf. Robinson 1992; Holbrook et al. 2009).

Do the cooperative behaviours shown in the experimental situation benefit the helpers directly, or are they altruistic? In other words, do the direct fitness costs of the behaviours exceed the fitness benefits, meaning that these net costs are compensated by indirect fitness gains, if the behaviour exhibited is adaptive? Previous studies showed that attack behaviour and digging are energetically costly, increasing energy use compared to an inactive state by four to six times (Grantner & Taborsky 1998). In addition, digging and defence make the actors conspicuous and may impair vigilance, which increases predation risk. It is unlikely that defence against *T. vittatus* that are no threat to helpers but are keen egg predators provides direct fitness benefits to helpers. However, there is an above-random chance that the beneficiaries of helpers' defence, that is, the brood produced by the dominant breeders, are relatives of small helpers (Dierkes et al. 2005). Therefore, a potential genetic basis of the defence behaviour of small helpers and juveniles against predators of eggs and larvae can be subject to kin selection. In contrast, the degree of relatedness between beneficiaries and large helpers does not exceed the population mean owing to the dynamics of territory ownership (Dierkes et al. 2005). Therefore, kin selection is an unlikely cause of a potential genetic basis of large helpers' cooperation. Instead, several experimental studies performed in both the field and the laboratory have suggested that large helpers pay to be allowed to stay in the territory of dominant breeders (Taborsky 1985; Balshine-Earn et al. 1998; Bergmüller & Taborsky 2005; Bergmüller et al. 2005a; Brintjes & Taborsky 2008). Removing sand from the breeding shelter, which was more often shown by large than by small helpers, could also provide direct fitness benefits, because it increases the space available for hiding if this is required to escape predators. However, large helpers rarely hide in the breeding shelter, because they are often not tolerated there and instead use their own shelters within the territory (Werner et al. 2003). Therefore, the high digging effort of large helpers is likely to be part of their reciprocal relationship with the dominant breeders (Taborsky 1985; Bergmüller & Taborsky 2005).

When the density of egg predators was experimentally increased, the average distance of helpers to the breeding shelter tended to be greater than in the control situation, and the time spent inside the shelter was reduced. This might indicate an increase in helper vigilance and a higher effort in egg predator deterrence. In some cooperatively breeding birds and mammals, vigilance is associated with coordinated sentinel behaviour (Gaston 1977; Rasa 1986; Bell et al. 2009), which involves guarding from a raised position (McGowan & Woolfenden 1989) and often alerting other group members to danger with the help of alarm calls (Clutton-Brock et al. 1999). In *N. pulcher* the sight of fleeing or defending helpers seems to alert other group members as well (personal observation). When a large predator posing a severe threat to helpers was experimentally introduced in an experimental set-up resembling ours, helpers stayed closer to shelter and hid more in comparison to a control situation without predators (Heg et al. 2004a).

The total amount of digging shown by group members when sand was added to the breeding shelter was higher in the egg predator treatment than in the control situation, implying that territory maintenance gains importance when the density of egg predators is high. This effect was strongest in male and female breeders, indicating that they might gain most from a safe breeding shelter when egg predators abound.

Mean shelter distance of helpers correlated negatively with group size, which might indicate competition for primary shelter access among group members. Potential benefits of staying close to

the breeding shelter include access to a safe retreat when threatened (Taborsky & Limberger 1981; Taborsky 1984), the opportunity to perform direct brood care (Taborsky 1984; Werner et al. 2003), antipredator defence by dominant group members (Taborsky 1984; personal observation), a potential for reproductive parasitism (Dierkes et al. 1999; Heg et al. 2006), and the opportunity to cannibalize breeders' eggs or larvae (Taborsky 1984, 1985; von Siemens 1990). We also found a negative correlation of group size with the foraging activity of helpers in the water column, which might reflect opportunity costs imposed by the increased need to stay close to the breeding shelter because of competition for space among group members (cf. Werner et al. 2003). This is also corroborated by the negative relationship between the amount of plankton and benthos feeding we found in small helpers, which points to a trade-off between these foraging techniques and the corresponding space use. In another field study involving a much greater range of group sizes, helpers in large groups fed at higher frequencies than helpers in small groups (Balshine et al. 2001). This discrepancy might point towards nonlinear effects. Experimental reduction of the number of group members did not affect feeding rates of helpers in the same natural population (Brouwer et al. 2005).

There was no dispersal of helpers in either treatment in our study, which resembles results from another experiment conducted in the same colony involving plankton density manipulation (Brintjes et al. 2010). In an earlier study using a similar experimental set-up (Heg et al. 2004a), helpers did disperse, however, but there the experimental period was twice as long (2 instead of 4 weeks) and the group sizes were larger, which might provide greater dispersal incentives.

In conclusion, our results suggest that the effort and task differentiation of group members in *N. pulcher* depend on demand, status and body size of group members. The specialization to perform certain tasks seems to reflect size-dependent differences in opportunity, efficiency or both among group members of this cooperatively breeding vertebrate, which bears a resemblance to the division of labour observed in eusocial insects.

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