Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints

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The theory of family-group dynamics predicts that group structure, helping behaviour and social interactions among group members should vary with the opportunities of subordinates to breed independently. We investigated experimentally whether unrelated mature helpers in the cooperatively breeding cichlid *Neolamprologus pulcher* reduce costly social and cooperative behaviour and choose to disperse and breed independently when offered vacant breeding sites. As predicted by the ecological constraints hypothesis, when breeding substrate was available, (i) helpers spent more time in dispersal areas and it was mainly large helpers that left the group to breed independently; (ii) all helpers invested less in costly submissive behaviours towards other group members and large helpers reduced help, supporting the 'pay-to-stay' hypothesis; and (iii) large helpers, particularly those that dispersed and bred, increased more in body mass in the treatment than those without breeding options, suggesting status-dependent strategic growth of helpers. We conclude that helpers of *N. pulcher* decide whether to stay and pay or disperse and breed in response to constraints on independent breeding.

1. INTRODUCTION

In cooperative breeders, subordinate group members help others to raise their offspring. Many studies have attempted to explain such behaviour by invoking natural selection (Skutch 1935; Woolfenden 1975; Taborsky & Limberger 1981; Taborsky 1984; Brown 1987; Stacey & Koenig 1990; Emlen 1995) and kin selection (Hamilton 1964) has been a powerful concept in this context (e.g. Emlen 1997). However, as pointed out recently (e.g. Cockburn 1998; Clutton-Brock 2002), direct fitness benefits alone may often explain the evolution of cooperative societies. This is supported by data showing that in some species relatedness of helpers and their beneficiaries is low (Dunn *et al.* 1995; Richardson *et al.* 2002; P. Dierkes, D. Heg, M. Taborsky, E. Skubic and R. Achmann, unpublished data) or the amount of help provided by subordinates is not modulated according to the level of kinship to the supported offspring (Magrath & Whillingham 1997; Clutton-Brock *et al.* 2000). In most cooperative breeders, delaying dispersal is regarded as a prerequisite of helping behaviour. However, the latter is not an inevitable consequence of staying (e.g. Ekman *et al.* 1994). Hence, the evolution of helping behaviour needs to be addressed at two different levels (Emlen 1984): (i) why do subordinates stay in their natal territory and forego their own reproduction and (ii) why do subordinates help dominants to raise offspring? Although these questions may need separate explanations, they must however be considered in parallel as they are closely linked (Cockburn 1998).

Three hypotheses have been proposed to explain why subordinates delay dispersal.

(i) The 'ecological constraints' hypothesis assumes that ecological factors set boundaries for helpers to disperse and breed independently (Selander 1964). Although experimental evidence is rare (Pruett-Jones & Lewis 1990; Komdeur 1992; Walters *et al.* 1992), this hypothesis has been widely accepted as an explanation for delayed dispersal (Koenig *et al.* 1992; Emlen 1997; Hatchwell & Komdeur 2000; but see Pen & Weissing 2000; Kokko & Ekman 2002).

(ii) The 'benefits of philopatry' hypothesis suggests that subordinates obtain fitness benefits from staying, e.g. by raising the production of kin, through inheriting the territory or increased survival chances (Taborsky 1984; Woolfenden & Fitzpatrick 1984; Stacey & Ligon 1991).

(iii) The 'life-history' hypothesis proposes that certain life-history traits such as longevity, low adult mortality or low dispersal predispose cooperative breeding when these traits result in a slow population turnover, as this limits the opportunities for independent breeding of subordinates (Arnold & Owens 1999; Hatchwell & Komdeur 2000; Kokko & Ekman 2002).

However, all three hypotheses are closely linked, as they differ mainly in the emphasis set on the costs and benefits of staying versus leaving.

Many hypotheses attempt to explain why philopatric group members show helping behaviour. They may either gain indirect fitness benefits from raising close kin, or direct fitness benefits by sharing in reproduction, inheriting the

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territory, or practising brood care (for a review see Emlen 1997). Alternatively, helping may increase the likelihood of being tolerated by the dominants in the territory ('pay-to-stay hypothesis'; Gaston 1978; Kokko *et al.* 2002). This principle could be a general mechanism for regulating group cohesion whenever fitness interests of dominants and subordinates are in conflict. As paying to stay will not be evolutionarily stable when subordinates attain higher fitness benefits from leaving, there are obvious parallels to reproductive skew theory (Kokko *et al.* 2002). For instance, restraint models propose that subordinates may reduce or cease participating in reproduction to avoid expulsion by dominants (Johnstone & Cant 1999; Hamilton 2004), which may be regarded as another way in which subordinates 'pay' to remain tolerated in the territory.

The 'pay-to-stay' concept intrinsically involves punishment as a means for dominants to control payment by subordinates (Clutton-Brock & Parker 1995). Although solutions to the question of when punishment should occur have been modelled recently (Kokko & Ekman 2002; Hamilton 2004), empirical studies addressing this issue in animal societies are scarce (Clutton-Brock & Parker 1995; see Fehr & Gächter (2002) for an example in humans).

Here, we report an experimental study testing simultaneously whether 'ecological constraints' and 'pay-to-stay' hypotheses might explain delayed dispersal and the amount of helping behaviour shown by subordinates in a highly social fish species, *Neolamprologus pulcher*. This group living cichlid belongs to the substrate-breeding Lamprologini and is endemic to Lake Tanganyika. Groups usually consist of a breeding pair and on average, five helpers of both sexes and different size classes (Balshine *et al.* 2001). Groups defend small territories along the rocky sublitoral zone and use holes and crevices for hiding and breeding (Taborsky & Limberger 1981; Balshine-Earn *et al.* 1998). Sexually mature helpers face costs when delaying dispersal, e.g. (i) reduced growth rates (Taborsky 1984), (ii) delayed reproduction (Taborsky & Limberger 1981) and (iii) increased energy expenditure as a result of helping and costly social interactions (Grantner & Taborsky 1998; Taborsky & Grantner 1998). Helpers share in territory defence, shelter maintenance and brood care (Taborsky & Limberger 1981; Taborsky 1984; Balshine-Earn *et al.* 1998). Within-group relatedness is low, especially between breeder males and large helpers, as breeders are often replaced (Taborsky & Limberger 1981; Stiver *et al.* 2004; P. Dierkes, D. Heg, M. Taborsky, E. Skubic and R. Achmann, unpublished data). Contrary to expectation, observational and experimental data from the laboratory and field (Taborsky 1985; Heg *et al.* 2004*a*) suggest that helpers attempt to stay as long as possible in the group territory, even when they have opportunities to disperse and reproduce independently. We thus created breeding vacancies to investigate whether subordinates disperse under *optimal* conditions for independent reproduction, including ample availability of potential breeding partners, low competition between dispersing helpers and absence of space competitors and predators.

Some evidence suggests that, in *N. pulcher*, helpers pay to be tolerated in the dominants' territory. Helpers that are not directly related to beneficiaries stay in the territory and continue to help them even if one or both breeders are replaced (Taborsky & Limberger 1981; Taborsky 1984).

Above a certain size, helpers are only tolerated in the territory when they are needed (Taborsky 1985). Temporarily removed helpers increased the amount of territory maintenance and defence after their return (Balshine-Earn *et al.* 1998), and helpers that were experimentally prevented from helping subsequently increased the amount of help provided (Bergmüller & Taborsky 2005).

In our experiment, standardized breeding groups were created in the laboratory and only helpers were able to use adjacent dispersal compartments. Half of these contained breeding substrate (treatment), while the other half did not (control). We tested four predictions of the 'ecological constraints' (i–ii) and 'pay-to-stay' (iii–iv) hypotheses. We predicted that: (i) helpers would disperse and breed independently if breeding substrate is available; (ii) large helpers would be more likely to disperse and breed successfully, as dominance is largely determined by size; (iii) helpers would reduce the amount of costly behaviours at home if independent breeding options were provided; and (iv) breeders would punish helpers reducing their helping effort.

2. METHODS

(a) *Experimental set-up*

The experiment was conducted from 3 July 2002 to 9 November 2002 in the laboratory of the Ethologische Station Hasli at the Institute of Zoology of the University of Bern with fish caught at the southern end of Lake Tanganyika at Mpulungu (Zambia) and their laboratory-reared offspring. Fish were introduced into a circular (ring-shaped) tank of 7200 l size, which was partitioned into smaller compartments (figure 1). The tank bottom was covered with sand (30 mm, 1 mm grain size), water quality was kept constant (see Taborsky 1984), temperature was $27 \pm 1\,^{\circ}\mathrm{C}$, and the light regime was 13 L : 11 D with a twilight period of 10 min in between. Commercial dry food (Tetramin) and frozen food (a mixture of daphnia, *Artemia salina* nauplia and chironomid larvae) were provided alternately once a day after observations.

Using opaque Plexiglas partitions, the tank was divided into eight independent sections containing four compartments with one breeding group in each (i.e. 32 groups in total), plus one dispersal compartment in between. Group and dispersal compartments within each section were divided by transparent Plexiglas partitions. Group compartments contained two flowerpot halves serving as breeding shelters. Each group consisted of a breeder pair and one large and one small helper (in total 128 fish). The fish were randomly chosen from different tanks with aggregations (i.e. groups without breeding shelters, fish were not reproducing). Body mass and standard length (SL) of all fish were measured before and after each experimental period (for procedures see Taborsky 1984). Breeders were more than 60 mm SL, with male breeders larger than females (as observed in the wild (Taborsky 1984; Balshine *et al.* 2001)). Small helpers were 35–42 mm and large helpers were 43–51 mm SL. The two helpers in each group differed clearly in size and were of opposite sex, so that in each section two groups had a large female helper with a small male helper, and the other two groups had a large male helper with a small female helper. We marked the fish individually by clipping the dorsal fin. Breeding groups were created artificially to rule out a potential influence of group composition and relatedness on the results of the experiment (see Taborsky (1984) for details and discussion of this methodology). The fish became accustomed
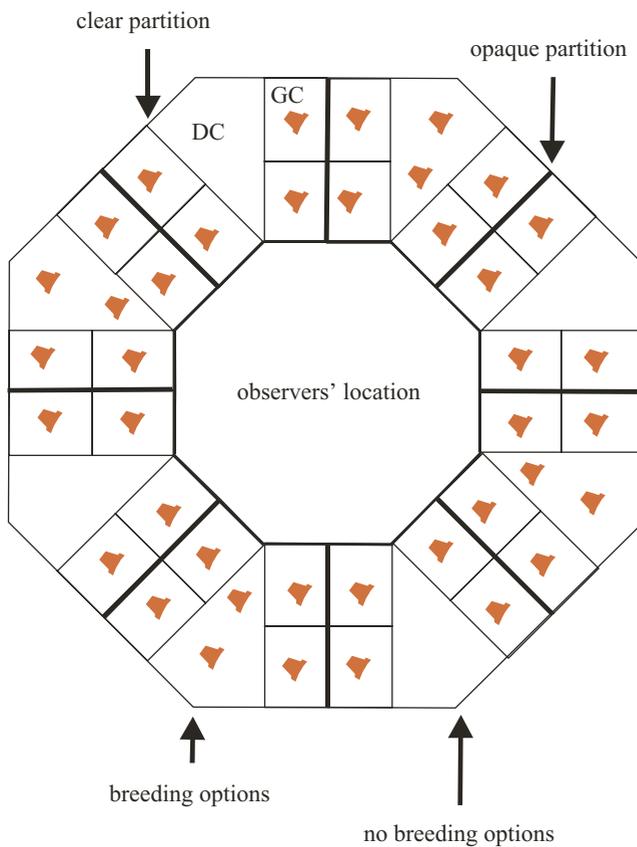
Figure 1. Experimental set-up in the full-glass circular tank, viewed from above. Observations were made from inside the ring (observers' location). The groups were located in the 32 group compartments (GC). Flowerpot halves served as breeding substrate. In the experimental phases, only fish of helper size could switch between group compartments and dispersal compartments (DC). In phase 2, the pot halves were moved into the dispersal compartments that did not contain pot halves in phase 1.

quickly to the experimental conditions, with the first group producing a clutch 5 days after it had been created.

Before starting observations, the fish were familiarized with the experimental situation for a period of 26 days. Helpers were trained for an additional period of 48 days to swim through dispersal slots connecting the group and dispersal compartments: helpers were allowed to pass through the slots into small plastic tanks and back to their home compartments, while the slots were too small for breeders.

(b) *Experimental procedure*

The experiment comprised two phases of 23 days each. In phase 1, half of the eight dispersal compartments contained flowerpot halves. Sections with pot halves alternated with sections without. In phase 2, the pot halves were switched between sections. After phase 1 all fish that had dispersed were moved back to their groups and allowed to acclimatise for 8 days before the start of phase 2. Once per day, on 21 of 23 days within each phase, we recorded whether the helpers were (i) in their group compartment, (ii) in another group's compartment or (iii) in the dispersal compartment.

Two observers (D.H. and R.B.) recorded focal observations of behaviour with the help of the software 'THE OBSERVER, v. 3.0' (Noldus, Wageningen, The Netherlands). Both observers monitored

each fish twice for 15 min in random order within each phase of the experiment. Recorded behaviours included: (i) helping behaviour, i.e. digging (removing sand from breeding shelters); and (ii) social interactions within the group, i.e. aggressive behaviour (overt aggression: mouth fighting, biting, ramming; restrained aggression: frontal approach, opercula spreading, fin spreading, head down display, S-shaped bend) and submissive behaviour (tail quivering, hook display, escape; for behaviour descriptions see Taborsky (1984)). Before each observation, both breeding shelters of the target group were carefully half-covered with sand to induce digging behaviour, which simulates natural conditions created by water movements (Taborsky & Limberger 1981). Before the start of the observations, the fish were allowed to acclimatize for 3 min.

To assess reproduction, we checked for new eggs in the pot halves every second day. Eggs were counted and removed to avoid changes in helping and aggressive behaviours as a result of the presence of new offspring. In 31 out of the 32 groups the breeders produced at least one clutch (range 1–4) during the experimental period. Eggs of broods produced by former helpers in the dispersal compartments were also counted and removed.

(c) *Data analyses*

For the analyses of social and helping behaviour only helpers that moved between home and dispersal compartments during each particular observation were included in the analyses, because in these cases we had certainty that the helpers had full information about the actual dispersal- and breeding options. Out of a total of 64 helpers, 30 were moving between compartments during the observations (11 in one treatment, 19 in both treatments; 18 large and 12 small helpers); and 17 helpers did so in the presence of pot halves, and 24 without.

To avoid pseudo-replication, we combined observations of helpers of the same size class within each section, because the behaviour of individuals within the same section might have been influenced by each other. As behavioural data were unbalanced because of individual differences in behaviour (i.e. not in all sections could large and small helpers help, interact with group members, or were moving between compartments), we analysed the social and helping behaviours with mixed-effects models using restricted maximum-likelihood methods, because this approach accommodates data that are missing at random (Rubin 1976). We included section and observer as random factors into all analyses to correct for undesired influences of these variables. Treatment and helper size were always included as fixed factors and interactions between the fixed effects were included only when significant. The time spent in the dispersal compartment (as obtained from the scan data) and the frequency of changing movements between dispersal and home compartments were included as covariates when this is mentioned in § 3.

We analysed daily scan data of helper locations and growth data of all helpers with repeated-measures ANOVAs including helper size as fixed and section as random factors. When additionally including the effect of reproductive status (whether helpers bred or not) or the time spent in the dispersal compartment into the analysis of body mass changes, we performed ANOVAs with treatment and helper size as fixed factors and section as random factor. The residuals of the analyses were tested for normality with Kolmogorov–Smirnov tests for goodness of fit. Distributions were tested for deviations from homogeneity of variances with the Levene's test. Non-normally distributed data were analysed non-parametrically. All statistical analyses were performed with SPSS (v. 11.0).

Figure 2. Frequencies of digging and submissive behaviour of helpers that changed between compartments during the observation. (*a*) Large helpers dug less in the presence of breeding options (grey shaded boxes), while small helpers did not change their digging behaviour (Mann–Whitney *U*-test, large helpers: $Z = -2.15$, $p = 0.03$; small helpers: $Z = -0.99$, $p = 0.35$). White boxes, no breeding option. The box plot shows the medians, upper and lower quartiles and whiskers indicate the highest and the lowest values excluding outliers. (*b*) Helpers reduced submissive behaviour (means±s.e.) in the presence of independent breeding options (black circles) (treatment: $F_{1,23} = 5.81$, $p = 0.02$; helpers size: $F_{1,23} = 0.49$, $p = 0.49$). Grey triangles, no breeding option.

3. RESULTS

(a) *Helper dispersal*

The daily scan data revealed that helpers spent more time in the dispersal compartments when shelters were offered for independent breeding than in the control situation (treatment: $F_{1,52} = 17.91$, $p < 0.001$), while helper size had no effect (helper size: $F_{1,52} = 0.005$, $p = 0.94$). Helpers moved less often between compartments when breeding options were available, and small helpers changed less often than large helpers (treatment: $F_{1,52} = 6.33$, $p = 0.02$; helper size: $F_{1,52} = 4.44$, $p = 0.04$).

(b) *Independent breeding of helpers*

In six out of eight dispersal compartments with breeding shelters, helpers formed pairs and bred independently (only one pair per compartment), whereas in compartments without breeding shelters helpers did not breed (Fisher's exact test: $p = 0.007$). Helpers originating from the same group never formed pairs. In total, 10 large and two small former helpers bred.

Larvae hatched in eight out of the nine broods of former helpers. The first helpers started to breed shortly after the dispersal slots were opened: after 8 days in phase 1, and after 4 days in phase 2. On average, the helpers bred for the first time within 12 days after providing independent breeding opportunities (i.e. after half of the treatment time, range $= 6$–23 days, $n = 6$ first broods; the other three broods were second broods of the same former helpers).

(c) *Helping and submissive behaviour*

Large helpers that changed between compartments during the observation (see § 2) dug significantly less often when breeding options were available, while small helpers did not change their helping behaviour (figure 2*a*). All helpers also reduced the amount of submissive behaviour towards other group members in the group territory when breeding options were available (figure 2*b*), but there was no difference between large and small helpers. As helpers moved less often when breeding options were available (see above), reduced submissive behaviour might have been a result of a reduced frequency of changing. However, when including the frequency of changes into the analysis, the effect of treatment was still significant (treatment: $F_{1,22} = 4.24$, $p = 0.049$; helper size: $F_{1,22} = 1.09$, $p = 0.31$; changes: $F_{1,22} = 3.46$, $p = 0.07$). Helpers did not receive more attacks in the presence of independent breeding options, but large helpers tended to receive more attacks than small helpers (treatment: $F_{1,23} = 0.90$, $p = 0.35$; helper size: $F_{1,23} = 3.09$, $p = 0.09$).
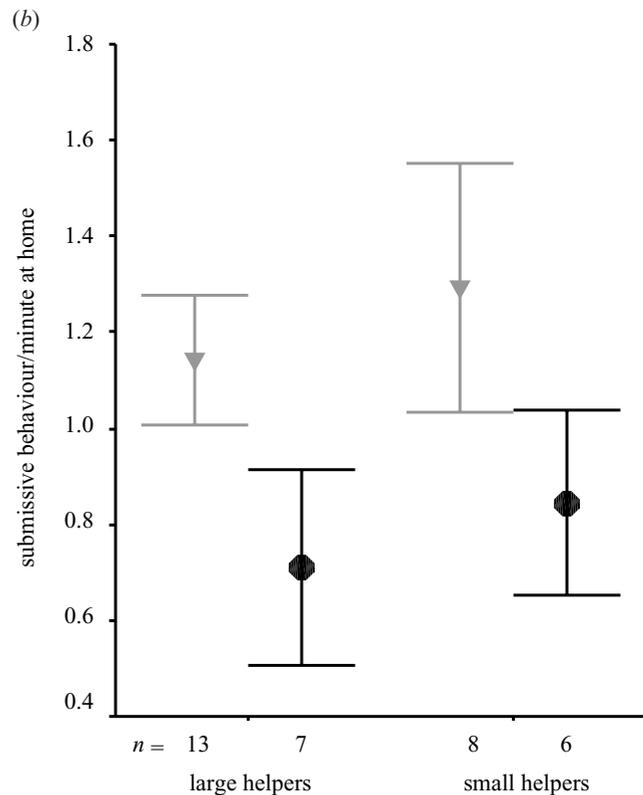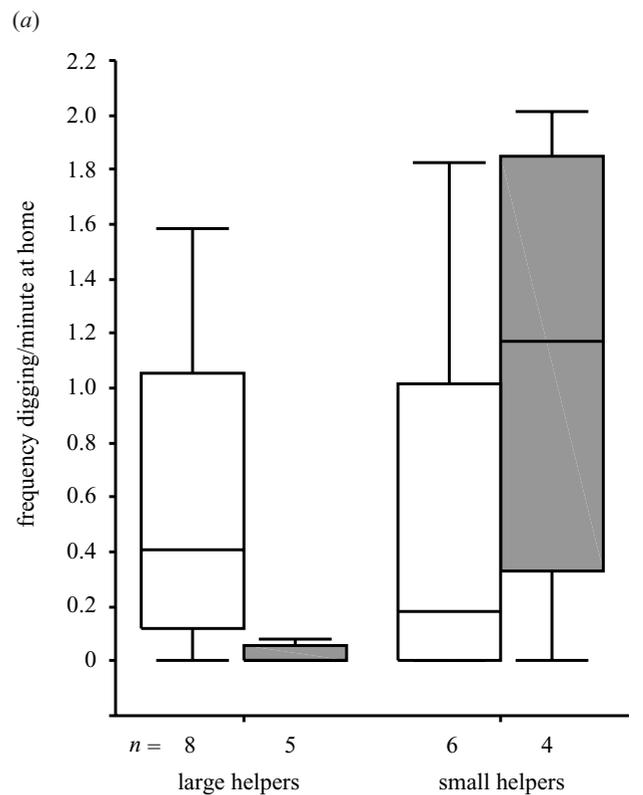
(d) *Helper growth and condition*

Helpers increased in relative body mass when breeding options were available (figure 3*a*) and small helpers increased relatively more in body mass than large helpers. We included the proportion of time spent in the dispersal compartment (scan data) into the analysis to check whether

(a)

(b)
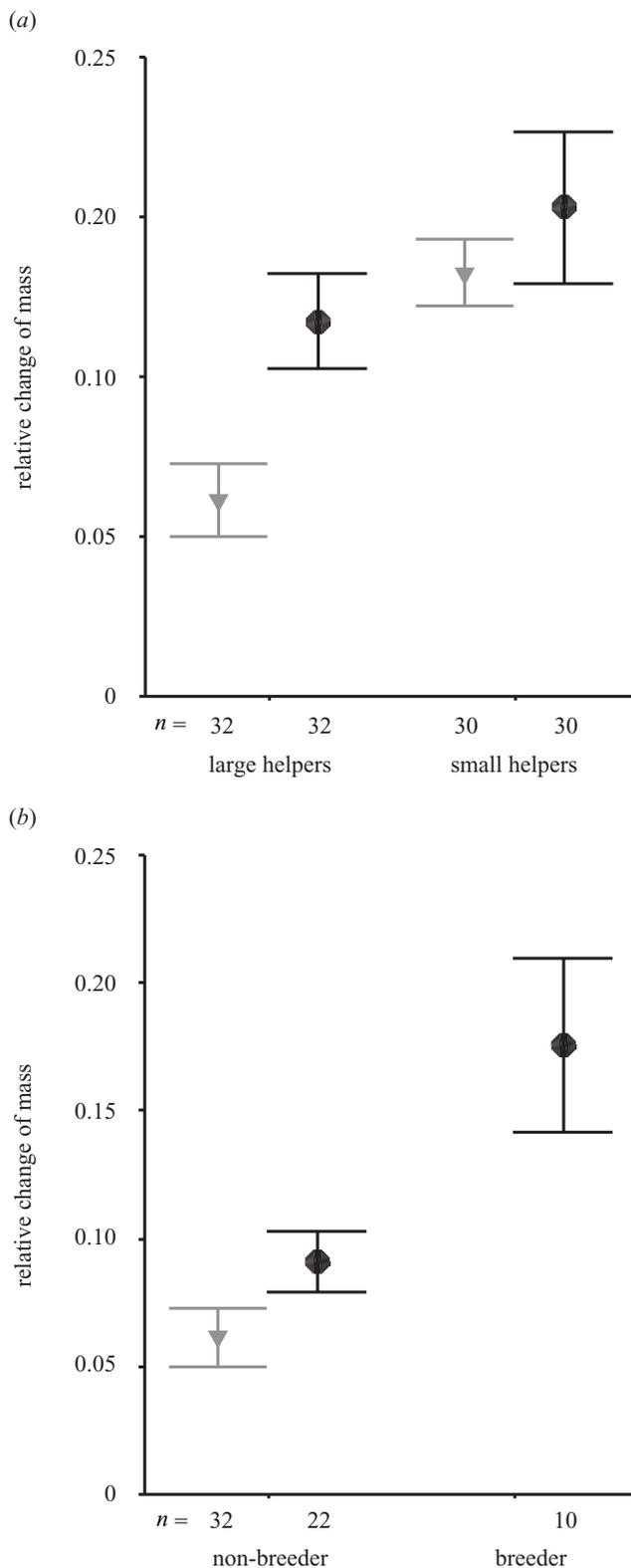
Figure 3. Increase of helpers' relative body mass (means±s.e.) depending on the availability of independent breeding options and reproductive status (only large helpers). Relative body mass is the proportional increase in mass based on the initial body mass. Grey triangles, no breeding option; black circles, breeding possible. (a) Helpers increased more in body mass when breeding options were available (treatment: $F_{1,53} = 4.52$, $p = 0.038$) and in general small helpers increased relatively more in body mass than large helpers (helpers' size: $F_{1,53} = 13.86$, $p < 0.001$). (b) When including reproductive status (whether helpers bred or not) into the analysis, large former helpers that were breeding increased more in body mass compared to large helpers that did not breed (status: $F_{1,54} = 6.77$, $p = 0.01$), while there was no significant treatment effect (treatment: $F_{1,54} = 2.32$, $p = 0.13$). However, a separate analysis of large helpers that were not breeding showed a trend for an increase in body mass in the presence of independent breeding options (treatment: $F_{1,45} = 3.87$, $p = 0.055$).

When analysing helper size classes separately, large helpers gained more weight when independent breeding options were available (large helpers, treatment: $F_{1,24} = 10.90$, $p = 0.003$), while small helpers did not do so (small helpers, treatment: $F_{1,22} = 0.21$, $p = 0.65$). When we considered whether large helpers bred or not as an additional factor, we found that large breeding former helpers increased significantly more in body mass than non-breeding helpers, while the treatment effect did not remain significant. However, when excluding former helpers that were breeding, large helpers still showed a strong trend to gain more in body mass in the presence of breeding options (figure 3b).

4. DISCUSSION

(a) *Dispersal and independent breeding*

Our experiment renders strong support for the ecological constraints hypothesis, as helpers spent more time outside the group territory and dispersed to breed independently when breeding opportunities were available. As predicted, mainly large helpers dispersed and bred successfully, as dominance is largely determined by size. Experimental evidence for the ecological constraints hypothesis is sparse and confined to a few species of birds (Pruett-Jones & Lewis 1990; Komdeur 1992; Walters *et al.* 1992). Probably the strongest evidence for the importance of ecological constraints so far has been found in Seychelles warblers (*Acrocephalus sechellensis*). When some individuals were transferred to a new island, the birds started to breed cooperatively only after all high-quality territories had been occupied (Komdeur 1992). Similarly, the results of our study suggest that the restricted availability of independent breeding opportunities may be a key reason for why subordinates of N. *pulcher* stay in the parental territory, which is considered to be a precondition for the evolution of cooperative breeding.

(b) *Pay-to-stay*

Large helpers that changed between compartments, and hence were fully informed about the available breeding options, helped less when shelters were present. Also, large and small helpers displayed submissive behaviour towards other group members less frequently when breeding

the increase in body mass was related to the time spent in the dispersal compartments, but there was no significant relationship between these variables (proportion of time in dispersal compartment: $F_{1,112} = 1.58$, $p = 0.21$). The same analysis with growth (SL) as the response variable did not reveal significant differences (treatment: $F_{1,51} = 2.12$, $p = 0.15$; helper size: $F_{1,51} = 0.139$, $p = 0.71$).

options were available. Apparently, helpers reduce their investment at home when given the opportunity to breed independently, which is predicted by the 'pay-to-stay' hypothesis. The latter also predicts that large helpers react more strongly to the treatment than small helpers, as large helpers are more likely to breed successfully on their own when this is possible. As expected, only large helpers helped less and increased more in body condition when breeding options were present, and most helpers dispersing to breed were large helpers.

Experimental tests of the 'pay-to-stay' hypothesis in vertebrates are scarce. In *N. pulcher*, evidence for 'pay-to-stay' was found in two studies. Field data (Balshine-Earn *et al.* 1998) showed that residents attack temporarily removed helpers when the latter are returned to their group's territories; and helpers that were experimentally prevented from helping (territory defence) subsequently increased their helping contributions (Bergmüller & Taborsky 2005). Indirect evidence for 'pay-to-stay' comes also from an experimental study in another cooperative breeder, the superb fairy-wren (*Malurus cyaneus*), where helpers were removed temporarily from the nest (Mulder & Langmore 1993). The dominant males attacked these helpers upon return, but only during the egg incubation and chick-feeding stages, i.e. when help was needed.

If costly helping and submissive behaviours of helpers benefit breeders, they should react to a decrease of these behaviours by punishing helpers. We did not find increased aggression when changing helpers helped less in the presence of breeding options. In the present study, helpers could choose between alternatives and adjust their behaviour and spacing according to the social and ecological situation. Therefore, it is perhaps not surprising that helpers did not receive more aggression from dominants when they reduced their helping contribution. Another study suggested that helpers of *N. pulcher* used helping and submissive behaviour for pre-emptive appeasement of dominant group members (Bergmüller & Taborsky 2005). Hence, if helpers can influence the amount of aggression received from dominants by acting pre-emptively, punishment might be generally difficult to detect.

(c) *Growth and condition*
Large helpers grew heavier in the presence of breeding options compared to the control situation, which appears to be a result of status-dependent strategic growth and reduced energetic investment at home.

Status-dependent strategic growth to avoid conflicts with dominants was proposed in *N. pulcher* (Taborsky 1984), and recently in clownfish (*Amphiprion percula*; Buston 2003). Helpers of *N. pulcher* grew more slowly and were in worse condition than same-sized controls that were breeding independently, suggesting that dominance affects growth (Taborsky 1984). A recent study confirms strategic growth in *N. pulcher* by showing experimentally that the largest male helpers grew more slowly when the size difference to the dominant male breeder was smaller (Heg *et al.* 2004*b*). In the present study, former helpers, that bred independently, grew heavier than non-breeding large helpers. Breeding former helpers were dominant in the dispersal compartments, so status effects may have increased growth and condition despite of the requirement to invest

energy into reproduction, territory defence and maintenance activities in an own territory.

A previous study showed that helping and submissive behaviour are costly. Helpers spend 3.1 and 6.1 times routine metabolic rates, respectively, for submissive behaviour (tail quivering) and territory maintenance (digging) (Taborsky & Grantner 1998). Thus, large helpers might have increased in weight because they invested less energy in helping and social interactions when breeding options were available. As body mass of large helpers that were not breeding tended to increase in the presence of breeding options, reduced investment at home might in part be responsible for the body mass differences between the treatments.

Although all compartments received about equal amounts of food, helpers in dispersal compartments could have received a greater share owing to a higher food/fish-mass ratio. However, food was provided *ad libitum* in all compartments and the time spent in the dispersal compartments did not correlate with the changes in body mass. Thus, it is unlikely that this possibility explains the observed differences in body mass dynamics.

5. CONCLUSIONS
In conclusion, we have shown that helpers of *N. pulcher* choose to disperse and breed independently if appropriate conditions are available, which confirms the importance of ecological constraints for delayed dispersal. Helpers adjust their helping and social behaviours according to the existence of alternatives to staying and paying. The increase in body mass of dispersing helpers suggests that, besides the costs of delayed reproduction, delayed dispersal and continued helping are energetically costly and helpers may strategically adjust growth to remain tolerated by the breeders. To our knowledge, this is the first experimental study showing that ecological constraints may influence concurrently two major decisions of subordinates in a cooperatively breeding vertebrate: whether to stay and how much to pay.

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