Extended safe havens and between-group dispersal of helpers in a cooperatively breeding cichlid

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Summary

In cooperative breeders, between-group dispersal of helpers is expected to occur if it increases their fitness. Genetic data suggest that helpers in the cooperatively breeding Lake Tanganyika cichlid *Neolamprologus pulcher* occasionally migrate into nearby groups where they again become helpers. We studied in the field how and why helpers migrate between groups by recording their ranging and social behaviours. We found that helpers spent 5.3% of their time visiting other groups, where they received similar low levels of aggression as within their home group. Large helpers visited other groups more often than small helpers and helpers visited other groups more frequently when the queue in their home group was large, suggesting that helpers with low chances to inherit the territory search for alternatives. Our data show that helpers may use other groups' territories as a refuge, as helpers actively sought shelter within territories of neighbouring groups when we experimentally increased the perceived risk of staying in their home territory. We observed two attempted and one successful case of 'voluntary' (i.e., strategic) between-group dispersal, and experimentally induced three helpers to disperse into other groups. By regular visits, helpers appear to establish familiarity and social relationships with nearby groups, which serve as 'extended safe havens' to hide from predators. In the long run frequent visiting behaviour may facilitate between group dispersal.

Keywords: cooperative breeding, between-group dispersal, social network, territory quality, biological markets, Cichlidae, *Neolamprologus pulcher/brichardi*.

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Introduction

The timing and destination of subordinate dispersal and the costs and benefits involved, are a major issue in the field of behavioural ecology and studies of cooperatively breeding vertebrates (Greenwood, 1980; Pusey, 1987; Johnson & Gaines, 1990; Komdeur, 1992; Emlen, 1997; Kokko & Ekman, 2002; Dingemanse et al., 2003; Gardner et al., 2003; Heg et al., 2004a; Stiver et al., 2004; Bergmüller et al., 2005). Several mutually non-exclusive hypotheses to explain how subordinates may increase their fitness by dispersing have been proposed, including obtaining a breeding vacancy, to avoid inbreeding (Pusey & Wolf, 1996), and to reduce competition with kin (Griffin & West, 2002). Dispersal costs may involve increased predation risk and the failure to find a suitable habitat to settle and breed. In general, models of cooperative breeding assume that subordinates have one of two life-history options, either (a) stay in the home territory and eventually inherit the territory (Kokko & Johnstone, 1999) or (b) disperse to acquire a breeding position (Kokko & Ekman, 2002). However, it has also been recognised that subordinates might pursue a third strategy: (c) strategically leave and join another group as a subordinate (Creel & Waser, 1994).

Although unrelated subordinates joining other groups has been described in many species (Reyer, 1980; Rood, 1987; Sapolsky, 1996; Whittingham et al., 1997; Field et al., 1999; Baglione et al., 2002; Schradin & Lamprecht, 2002; Gardner et al., 2003; Fedigan & Jack, 2004), the causes and consequences of this alternative strategy have been rarely addressed (Alberts & Altmann, 1995; Baglione et al., 2002; Jack & Fedigan, 2004). Individuals incur various costs when staying in a group as subordinate. By migrating to another group, subordinates might increase their fitness if (1) they are able to participate in reproduction thereby avoiding inbreeding depression (Whittingham et al., 1997; Baglione et al., 2002), (2) the target group contains a smaller subordinate queue for the breeding position, or when the subordinate can obtain a higher position in the queue (Ens et al., 1995; East & Hofer, 2001; Kokko & Ekman, 2002), (3) there is reduced within-group competition due to e.g. a smaller group size or higher territory quality (Clutton-Brock, 1998; Werner et al., 2004), or (4) due to increased survival, e.g. because of active protection by other group members (Taborsky, 1984; Clutton-Brock et al., 1999; Heg et al., 2004a). (5) Finally helpers may have a lower workload in other groups e.g. if subordinates need to help less to be allowed to stay

in the group (i.e., the 'pay to stay hypothesis' (Gaston, 1978; Taborsky, 1984; Taborsky, 1985; Balshine-Earn et al., 1998; Kokko et al., 2002; Bergmüller et al., 2005; Bergmüller & Taborsky, 2005; Hamilton & Taborsky, 2005)).

However, between-group dispersal should only be expected when the acquired benefits will outweigh the benefits from staying and helping in the current group (Kokko & Lundberg, 2001). Also, members of the potential new home group may accept additional group members only when a further helper provides net benefits for the residents (Taborsky, 1984) which outweigh potentially increased costs e.g. due to competition with the residents for reproduction or a critical resource such as food or shelter space.

The option to strategically join another group has important consequences for our understanding of helping and social structure in cooperatively breeding species, and we may need to adopt a more dynamic view of group living than previously thought. For instance, transactional models of dominant-subordinate interactions (Johnstone, 2000; Kokko et al., 2002; Hamilton & Taborsky, 2005), developed to explain partitioning of reproduction, subordinate dispersal, and helping behaviour, might need adjustments to account for strategic subordinate between-group migration. Moreover, the option to strategically disperse between groups implies a potential to choose between different group memberships. Under such conditions biological market theory (Noë & Hammerstein, 1995; Noë, 2001) predicts that helpers may trade their helping contributions for being accepted in a territory that provides improved conditions.

However, before actual dispersal, one would expect subordinates to sample their environment, e.g. by visiting neighbouring groups. Visitors might gain public information (Valone & Giraldeau, 1993) about the availability and quality of nearby vacancies or potential reproductive partners, or about the likelihood of successful dispersal, i.e. 'prospecting behaviour' (Reed et al., 1999; Doligez et al., 2002). Also, visits might serve to establish familiarity and social relationships with the members of neighbouring groups, increasing the likelihood of future acceptance. A social network may enable individuals to use nearby territories as 'safe havens' to hide from predators (Kokko & Ekman, 2002), to safely use large areas to gather information or for foraging, thereby creating 'extended safe havens'. Social relationships with other groups may additionally provide 'insurance retreats' for subordinates in case of expulsion from the home territory or dissolution of the group.

Neolamprologus pulcher is an excellent study system to address these issues as visiting and dispersal behaviour can be observed in the wild, a possibility that is rarely feasible with other cooperatively breeding vertebrates. Within-group relatedness is relatively low, especially between breeder males and large helpers, as breeders are often replaced (Taborsky & Limberger, 1981; Dierkes et al., 2005). Helpers risk expulsion from the group when participating in reproduction (Dierkes et al., 1999; Skubic et al., 2004) or when they are size-matched to the new breeders (Balshine-Earn et al., 1998), which appears to be the main reason why helpers leave the group (Taborsky, 1985; Dierkes et al., 1999). Under optimal conditions, mature helpers breed independently when given access to additional breeding shelters (Bergmüller et al., 2005). However, predation pressure may severely limit this possibility in nature (Heg et al., 2004a). Helpers occasionally migrate into other groups (3.5% immigrant helpers detected by microsatellite markers: Stiver et al., 2004; Dierkes et al., 2005). Since *N. pulcher* is able to recognise individuals (Hert, 1985; Balshine-Earn & Lotem, 1998) and strangers are usually attacked (Taborsky, 1984; Hert, 1985; Taborsky, 1985; Bergmüller & Taborsky, 2005), we predict that helpers will build up social relationships with group members of potential new home groups before immigrating. As yet, it is unclear whether under natural conditions between-group dispersal of helpers takes place only after expulsion or whether helpers may indeed migrate 'voluntarily' (i.e., strategically) to other groups.

In this study we investigated helper ranging and dispersal behaviour in a natural population in the Lake Tanganyika. (1) We determined parameters of group composition and group territory quality, which might influence the benefits of helpers when staying in a particular group. (2) We observed the ranging behaviour of individually marked, sexually mature helpers to determine whether they visit other groups depending on potential immediate benefits (survival), future benefits (queuing for the breeding position) or constraints (dispersal costs). Furthermore, we analysed the social behaviour when helpers visited other groups to investigate whether social relationships are established with neighbouring groups. We expect that helpers should visit mostly nearby territories with better territory quality (more shelters) and smaller queues of helpers than in their home group. (3) We experimentally increased the risk of helpers at home and tested whether they would take refuge in nearby groups. (4) Finally, we observed natural and induced dispersal of helpers to test whether they dispersed to previously visited groups.

Methods

Study species, population, subjects and general methods

N. pulcher is a highly social cichlid belonging to the substrate-breeding Lamprologini and is endemic to Lake Tanganyika. It lives in family groups consisting of a breeding pair and on average five helpers of both sexes and different size classes (Taborsky & Limberger, 1981; Balshine et al., 2001). Groups defend small territories along the rocky sub-littoral and use holes and crevices for hiding and breeding. Sexually mature helpers face various costs when delaying dispersal such as reduced growth rates (Taborsky, 1984; Heg et al., 2004b), delayed reproduction (Taborsky, 1985; Bergmüller et al., 2005) and increased energy expenditure due to helping and costly social interactions (Grantner & Taborsky, 1998; Taborsky & Grantner, 1998). Helpers participate in several cooperative tasks including territory defence and maintenance, and brood care. Experiments in the laboratory (Taborsky, 1985; Bergmüller et al., 2005; Bergmüller & Taborsky, 2005) and field (Balshine-Earn et al., 1998) suggest that helpers pay by helping behaviour for being allowed to stay.

We studied the ranging and dispersal behaviour of *N. pulcher* by SCUBA diving at the south end of Lake Tanganyika at Kasakalawe point near Mpulungu, Zambia (8°46.849′S, 31°04.882′E) from 20 February until 7 April 2003. The study population consisted of a colony of 32 groups at 9 m depth. All territories were marked with numbered rocks. Six of the groups were harems with one male occupying the breeder position in several adjacent groups. We created a grid system of 2×2 m squares with help of ropes (total area of 110 m^2), covering the whole colony. We mapped all territories and captured 25 sexually mature fish from 17 groups, by chasing them into plexi-glass tubes. To minimise disturbance, we caught only one or two fish per territory. One day after marking, we found that all marked fish were accepted back in their groups, which confirms that disturbance was indeed low. We measured the standard length (SL) of the fish, determined their sex by inspection of the genital papilla and marked them individually by injecting acrylic paint into their scale pouches, and by taking up to three fin clips at six different positions on the dorsal and anal fins. Additionally, we observed four fish that were individually recognisable by unique body characteristics. In total, we observed 29 individually identifiable fish and recorded ad libitum

whether and when they were observed in the home or in another territory (total 151 observations of visits during 56 hours observation time). We counted the number of territories up to 130 cm away from the brood chamber and measured the distance to the nearest neighbouring territory.

Measures of territory quality

In our study area, the brood chambers of *N. pulcher* were typically located in cavities created by one or more larger rocks (>20 cm edge length). We estimated territory quality in terms of available shelters of all the territories within a radius of 30 cm around the brood chamber by (1) counting the number of rocks in three size classes: small (<10 cm maximum edge length), medium (10-20 cm) and large (>20 cm). The number of rocks has previously been found to affect the number of group members a territory can harbour by an experimental rock-removal experiment (Balshine et al., 2001), as it influences the number of potential shelters available. (2) We also measured the number of effectively available shelters as this appears to be further determined by three other factors, i.e. (a) the size of the rocks, (b) the arrangement of the rocks and (c) the number of cavities created by the group members through digging.

Focal behavioural observations

We observed 22 focal helpers for 30 min each (twice for 15 min) and one helper for 45 min (three times for 15 min) and noted ranging and social behaviours (total 705 minutes observation time). Observations were performed randomly between 9:00 and 17:00 on different days (1-7 days between consecutive observations). The focal helpers were from 15 groups, 1 group with 3 helpers, 6 groups with 2 helpers each and 8 groups with 1 helper each.

The frequency of the following behaviours were recorded and lumped into four broad categories: (1) helping behaviour (digging and territory defence against conspecific and heterospecific intruders); (2) overt aggressive behaviour (mouth fighting, biting, ramming); (3) restrained aggression (frontal approach, opercula spreading, fin spreading, head down display, S-shaped bend); and (4) submissive behaviour (tail quivering, hook display, escape) (Kalas, 1975; Taborsky, 1984). We also noted the respective interaction partners of the focal helper and the time (in seconds) spent inside the home territory (within the 60 cm radius around the brood chamber), visiting another

territory, or elsewhere (outside a 60 cm range of any territory). When the focal was inside a territory, we noted the time spent at three different locations: (a) inside breeding shelter (i.e., shelter used by both breeders), (b) at territory centre (30 cm radius around breeding shelter, but not inside of it), or (c) territory periphery (between 30 and 60 cm radius around breeding shelter).

Experimental increase of the costs of staying in the territory

To determine whether helpers use other groups' territories as refuge in case of increased costs in the home territory, we experimentally increased the perceived risk of staying in the territory. We chased the focal helper from its home territory with a fish dummy for up to five times in immediate succession until it moved out of the territory (outside the territory periphery). The dummy was a large grey plastic fish model (SL = 12 cm), resembling a large piscivore Lamprologine cichlid, which was attached to a plexi-glass stick of 1 m length. About 10 seconds were allowed between two successive chases and the treatment was terminated after a maximum period of two minutes. Most fish (14 of 15) left the territory after two or three chases and only one fish did not leave the territory at all (after 5 chases). After the focal fish left the territory we observed the ranging behaviour and noted the number of territories the focal helper visited, the time and location (brood chamber, centre, periphery) spent in other groups' territories and the time till the observed fish returned to its home territory. As a control treatment, the focal fish was gently escorted out of the 60 cm radius range of the territory with a plastic plate and subsequently the same parameters were noted. The experiment was performed with 15 helpers of 15 different groups, and the control and risk treatments were executed in random order (8 of the fish were subjected to the risk treatment first and the other 7 were first subjected to the control). The second treatment was performed one to three days after the first treatment.

Enforced dispersal by increased costs at home

To induce helpers to switch to another group, we removed helpers temporarily from their group. This method is well suited to induce involuntary dispersal as previous experiments have shown that other helpers sometimes (29% of the cases) expelled temporarily removed helpers when they were released

back to their group after 4 to 7 hours (Balshine-Earn et al., 1998). We removed 12 marked helpers temporarily from their group on the 1st or 2nd of April 2003 and kept them in 4 large underwater cages ($50 \times 50 \times 50$ cm) in groups of 3 individuals and fed them daily with commercial fish food (Tetramin) until release within their territory either 3 or 4 days later (all were released on the 5th of April 2003). The helpers were observed immediately after release for 10 min and the fate of the helpers was checked two days later when they were again observed for 10 min. In pilot experiments we increased the costs of three helpers in their home territory by covering their individual shelters (Werner et al., 2004) with sand, which caused them to re-excavate their shelters. After one group gradually dissolved we discontinued this treatment as it may have disturbed the group.

Data analysis

Helper visiting behaviour was analysed in two steps. First, we analysed whether visiting behaviour of helpers depended on characteristics of the home or target group (any other group in the study colony). Only helpers visiting a target group at least once were included. As it is equally informative when other territories were not visited, we included all territories of the colony (also receiving 0 visits) into the analysis. We included all independent variables of the helper, the home group features, and the target group features and related these to the dependent variable 'number of visits' using Poisson Regression Linear Models in the software R (Crawley, 2002). Independent variables included were: focal helper body size (standard length SL mm), helper sex, helper distance to the target group (ln-transformed), and for both the home group and the target group: the body size of breeder female, the number of shelters, total number of helpers, total number of large helpers (>35 mm SL), the number of helpers larger than the marked helper (denoted with 'queue length') and the territory competition index (total number of helpers divided by the number of shelters). The number of large helpers and the total number of helpers might influence visiting behaviour in different ways. To determine the most important factors affecting visits, we included them both into our analysis although they are not independent in a strict sense. Since helpers preferably visited nearby target groups (see Results), one might argue helpers are not free to sample all target groups inside the colony. To control for this potential confounding effect we included the

distance to the visited territory into the analysis. Also, relative measures of target groups compared with home groups were entered into the model and tested for significance. As sex and body size of the marked helper and the body size of the breeder male could not be determined in a substantial proportion of cases, we excluded the respective values from all models thereby reducing the sample size from 841 to 406 cases (pairwise group versus target group visits including the cases of 0 visits to other groups), comprised of 14 helpers in total.

Second, we analysed whether helpers spent more time in a visited group depending on the same independent variables as listed in the first analysis, using a multiple Linear Regression with forward selection of terms in the software SPSS 11.0. Actual visiting time was only determined during the 15-minute focal observations, and multiple visits to the same group during one such observation might not be independent events. Therefore, the total time spent in a visited group (in seconds) during an observation was used as the dependent variable, with 28 visits by 16 helpers in total (1 to 4 visits per helper, the random effect of individual helpers was not significant, $F = 0.40$, df $= 15$, $p = 0.95$, when added to the final model using a separate GLM). We ln-transformed the number of large helpers in a group because this procedure significantly improved the model fit as it accounts for exponentially declining visitation time depending on the number of helpers in the target group.

All other data were analysed with parametric statistics when their distributions did not deviate from normality (Kolmogorov-Smirnov tests), and in case of comparison between treatments, when the variances of the two treatments did not differ significantly. Otherwise, non-parametric tests were applied.

Results

Group size, group composition and competition

Sizes and composition of the groups in our study colony were highly variable. Groups contained 3 to 25 helpers (mean $\pm$ SD: 9.93 ± 5.07, $N = 29$), including 1 to 10 large (>35 mm SL) presumably sexually mature helpers (mean $\pm$ SD 3.70 ± 2.13, $N = 28$). Group size was positively correlated with the number of large helpers (Pearson $r = 0.87$, $p < 0.001$, $N = 28$), size
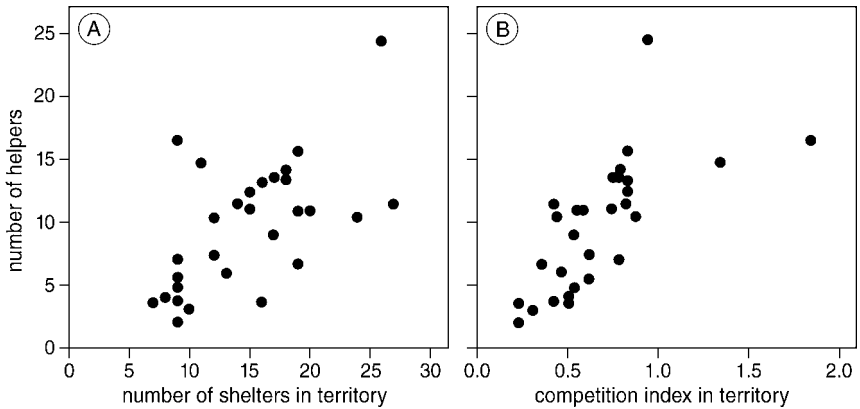
Figure 1. The number of helpers in a group correlates positively (A) with the number of shelters in the territory centre (Pearson $r = 0.58$, $p = 0.001$, $N = 26$) and (B) with competition index (number of helpers divided by the number of shelters, Pearson $r = 0.683$, $p < 0.001$, $N = 28$).

of the breeder male (Pearson $r = 0.40$, $p = 0.04$, $N = 26$) and the number of shelters (Figure 1a), but not with size of the breeder female (Pearson $r = 0.25$, $p = 0.19$, $N = 28$) or the number of rocks in the territory (Pearson $r = -0.1$, $p = 0.62$, $N = 28$). Moreover, the competition index increased with group size, showing that larger groups had relatively lower numbers of shelters available per individual group member (Figure 1b). This means that in very large groups, group members had to share their shelter with other group members, whereas in small groups (<15 individuals) helpers usually had at least one individual shelter available for hiding upon a predator attack.

Ranging and visiting behaviour

Based on the ad libitum observations, helpers visited on average 3.3 different groups (range: 1-8 groups, $N = 29$ helpers, 151 visits observed in total). Of the observed helpers, 86% (25/29) visited at least one other group. Surprisingly, aggressive responses of resident group members to these visitors were very rare, i.e. they were only observed in 5 out of 151 visits (3.3%).

In total, 15 of 23 focal helpers (65%) visited at least one other group during 30 minutes of observation time. Helpers visited on average 2.38 different groups per hour observation time (28 visits in 705 min observation time), but spent most of their time (87.0%) in their home territory. There they spent

4.0% inside the breeding shelter, 65.0% close to it (i.e., within the territory centre) and 18.0% in the territory periphery. Helpers spent 7.7% of their time outside of any territory (feeding or travelling to nearby territories), and 5.3% of time in other groups' territories (3.7% in the periphery and 1.6% in the territory centre). Helpers received little aggression: 21 aggressive acts (attacks and aggressive displays) from helpers and 2 from breeders during a total time of 613 min in their home territory and 5 aggressive acts from helpers and 2 from breeders during 35 min total time in other groups' territories. The rate of aggression received was similar inside their home territory and in visited territories (median values 0.5/min (range 0-3.8/min) vs 0/min (range 0-102.9/min), Wilcoxon matched-pairs signed ranks test, $N = 15, z = -0.89, p = 0.37$). They also showed similar levels of submissive behaviour inside their home territory compared to the visited territory (median values: 0/min (range 0-1/min) vs. 0/min (range 0-26.8/min), $N = 15, z = -1.26, p = 0.21$).

Helpers that visited other groups did not receive more aggression at home than helpers that did not (Figure 2). However, helpers that visited other groups showed significantly more submissive behaviour at home than helpers that did not visit other groups (Figure 2). Helpers were not helping in other
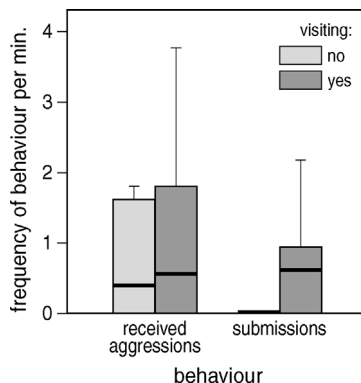

Figure 2. Social behaviour of helpers that visited other groups and those that did not, when helpers were at home. Shown are the boxplots with medians (bold line), 25% and 75% quartiles (boxes), 5% and 95% quartiles (lines with caps). Both types of helpers received similar levels of aggression (Mann Whitney U-test, $N_{\text{visiting}} = 15, N_{\text{not visiting}} = 8, U = -0.342, p = 0.73$), but helpers that visited other groups performed more submissive behaviour towards other group members of their own group than helpers that always stayed at home ($N_{\text{visiting}} = 15, N_{\text{not visiting}} = 8, U = -2.429, p = 0.02$).

groups, except when in the process of immigration (one observed helper, see below).

Which helpers visited which groups?

As expected, helpers performed more visits to nearby groups and large helpers visited other groups more often than small helpers did (Table 1). Also, helpers visited other groups more frequently when the queue in their home group was large and helpers tended to visit other groups more often when their home group contained less helpers (Table 1). Unexpectedly, the analysis also showed a positive effect of the number of large helpers in the target group on the number of visits (Table 1). The distance to the target group had the highest effect on the number of visits (Table 1, Figure 3), whereas the other independent variables increased the frequency of visits only marginally (see coefficients in Table 1).

   Using only the data of the 15 min focal observations, in the second analysis we determined whether the time spent inside the visited territories was influenced by helper SL and sex, the distance to the target group, and characteristics of the home group and the target group, i.e. all the variables in-

Table 1. Poisson Regression Model explaining the largest amount of variation in the number of visits helpers performed to groups. Null Deviance: 363.45, df = 405; Residual Deviance: 250.26, df = 400.

Independent variable[1]	z-value	df	p	Coefficient $\pm$ SE
Constant	-2.75	1	0.006	-5.566 ± 2.027
Helper size (SL mm)	2.67	1	0.007	0.126 ± 0.047
Ln (distance to group, in m)	-9.26	1	<0.0001	-1.262 ± 0.136
Home group				
Queue length[2]	2.45	1	0.015	0.173 ± 0.071
Total number of helpers	-1.84	1	0.066	-0.093 ± 0.051
Target group				
Number of large helpers	2.37	1	0.018	0.126 ± 0.053

[1] Variables removed (in brackets non-significant p-values when entered in the model, home group/target group/relative measures, respectively, where applicable, values with '−' represent the significant values shown in the table): helper sex (0.20), the body size of breeder female (0.69/0.15/0.45), the number of shelters (0.38/0.87/0.40), total number of helpers (−/0.30/0.76), total number of large helpers (0.21/−/0.21), queue length (−/0.86/0.86) and the competition index (0.68/0.61/0.19).

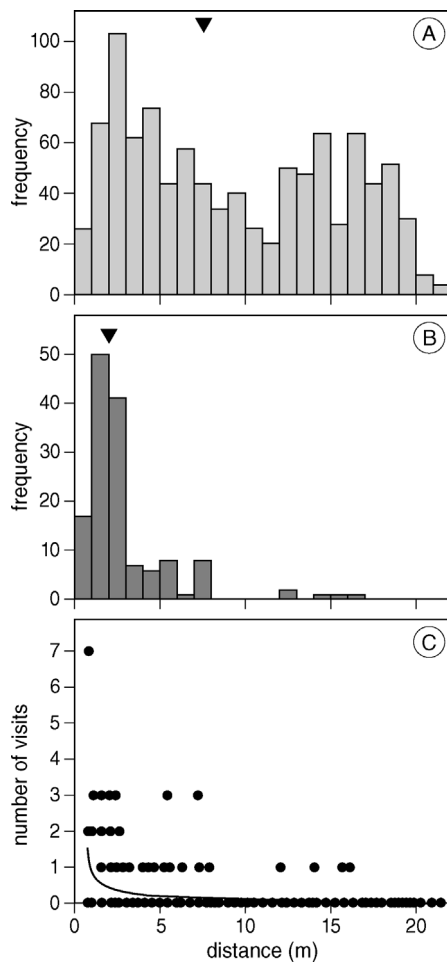[2] Queue length: number of helpers larger than focal helper.

Figure 3. The number of helper visits depended on the distance to the target group in *N. pulcher*. (A) For comparison, pairwise distances between all groups ($N = 992$ of 32 groups). (B) Helpers visited predominantly nearby groups: depicted are distances travelled between the home group and the visited group ($N = 143$ visits of 29 marked helpers). (C) Frequency of visits depending on the distance to the target territory ($N = 406$ pairwise distances between the territory of marked helpers and all target territories). The fitted line is based on the Poisson regression model presented in Table 1, controlling for the average effect of the other independent variables (i.e., coefficient × mean of the independent variable, summing for all independent variables in the model).

cluded in the first analysis. A stepwise forward selection Regression Model showed that helpers visiting distant groups tended to show shorter visitations (Table 2, Figure 4a) and there was a significant negative effect of the number of large helpers in the target group on visiting duration (Table 2, Figure 4b).

Table 2. Regression Model of the duration of group visits (in seconds) of helpers.

Independent variable	t-value	df	p	Coefficient $\pm$ SE
Constant	5.17	1	<0.001	93.87 ± 18.17
Ln (distance to group, in m)	-1.84	1	0.078	-22.68 ± 12.32
Target group				
Ln (number of large helpers)	-2.82	1	0.009	-32.95 ± 11.68

$N = 28$, $R^2 = 0.26$, Regression MS $= 5048.2$, Residual MS $= 1151.4$, $F_2 = 4.39$, $p = 0.02$. Variables removed (in brackets p-values when entered in the model, home group/target group/relative measures respectively, where applicable, value with '$-$' represents the significant values shown in the table): the body size of breeder female (0.18/0.55/0.62), the number of shelters (0.78/0.93/0.69), total number of helpers (0.83/0.38/0.74), total number of large helpers (0.56/$-$/0.75), queue length (0.65/0.79/0.57) and the competition index (0.66/0.30/0.66). Queue length is the number of helpers large than the focal helper. Due to the low number of sexed helpers in this sample ($N = 14$), helper sex was not tested in this model.
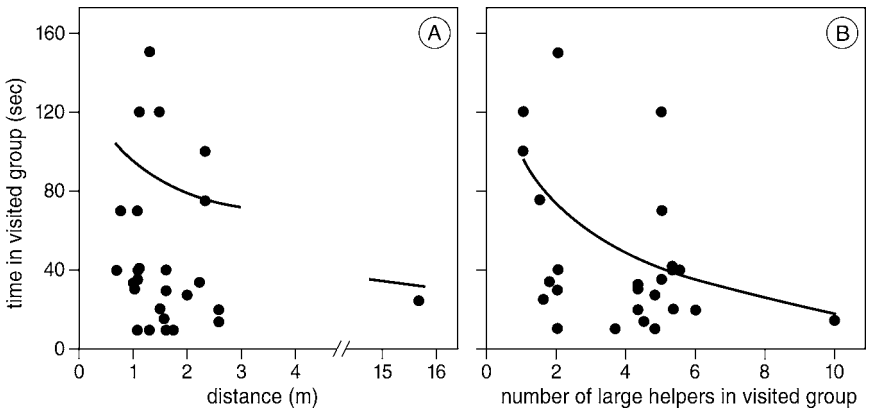

Figure 4. The time spent in the visited territory in relation to (A) the distance between the home group and visited group (marginally non-significant) and (B) the number of large helpers in the visited group. The fitted line is from the regression model presented in Table 2, controlling for the average effect of the other independent variable (i.e., coefficient $\times$ mean of the other independent variable).

Risk treatment

Focal helpers spent more time outside their home territory in the risk treatment than in the control treatment (Figure 5a), they performed more visits to other territories (median values: 1 (range 0-2) vs 1 (range 0-10) visits, Wilcoxon test, $N = 15$, $z = -2.23$, $p = 0.03$) and tended to stay closer to the centre of the visited territories (Wilcoxon test, $N = 15$, $z = -1.81$, $p = 0.07$) when perceived risk was high. Helpers stayed on average longer in other groups' territories during the risk treatment, than in the control treatment (median values: 5 (range 0-30) vs 40 (range 0-215) sec, Wilcoxon test, $N = 15$, $z = -2.80$, $p = 0.005$) and spent a higher proportion of their time outside of the home territory within other groups' territories (Figure 5b).

'Voluntary' between-group dispersal of helpers

One helper was observed during the process of immigration into another group. The latter consisted of the breeders and only one large helper who had been individually marked and observed before the immigrant appeared. The new helper continued to change between the two groups for four days.
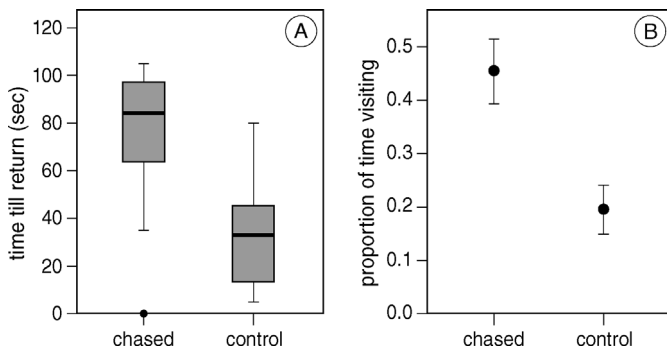

Figure 5. (A) Total time the helpers spent outside of their home territory (60 cm radius around brood chamber) after an experimental increase of perceived risk at home and after the control treatment. Helpers spent more time outside the group territory in the risk treatment compared to the control treatment (Wilcoxon's test, $N = 15$, $z = -3.30$, $p = 0.001$). Shown are the boxplots with medians (bold line), 25% and 75% quartiles (boxes), 5% and 95% quartiles (lines with caps) and one outlier (black dot). (B) Proportion of time visiting other territories after helpers experienced an increase in perceived risk at home and in the controls. Helpers spent a larger proportion of time visiting other groups in the risk treatment compared to the control (Paired sample t-test, $N = 14$, $t = -3.91$, $p = 0.002$). Shown are means ± SE.
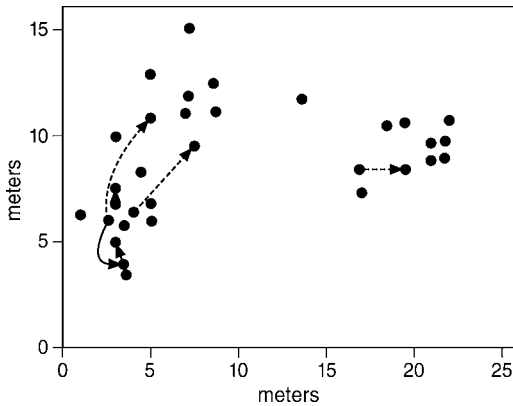
Figure 6. Spatial distribution of group territories in the study area. Arrows with solid lines represent attempted or successful voluntary between-group dispersal events, dotted lines represent experimentally forced emigrations from the group, which resulted in immigration to another group.

It had many social interactions and helped (digging) in both groups until it stayed in the new group permanently. Two other helpers who attempted to stay in a group were chased away by same-sized helpers after prolonged fights, and in the end were not successful in migrating to the new groups (Figure 6).

'Induced' dispersal (removal experiment)

We temporarily removed 12 helpers, which were released back into their territory after 3 or 4 days of confinement. We expected to induce dispersal and hypothesised the temporarily removed helpers would disperse to the group they had previously visited most when not reaccepted at home. However, contrary to previous experiments (Balshine-Earn et al., 1998), most of the helpers (10 out of 12; 83%) were reaccepted in their original territory. Immediately upon release, all ten reaccepted helpers showed vigorous submissive displays to the breeders and the larger helpers in the group, and no overt attacks were observed. The two unaccepted helpers changed to another group (Figure 6). Both stayed on the periphery of their new group, one of them at the previously most often visited group. One further helper moved to another group at the other edge of the colony after its individual shelter had been covered with sand in a pilot experiment. In total, six helpers dispersed or attempted to disperse into another groups' territory, 3 did so voluntarily (as described above) and 3 were induced to emigrate from their home

group (Figure 6). Of these helpers, three chose as target group the one they had previously visited most often. Helpers that strategically dispersed or attempted to disperse into another group chose groups that were closer to the home group than helpers that were experimentally enforced to emigrate and join another group (Mann Whitney U test, $N_1 = 3$, $N_2 = 3$, $U = -1.96$, $p = 0.05$).

Discussion

Our results on visiting behaviour strongly suggest that helpers in *N. pulcher* maintain social relationships with neighbouring groups, as helpers were rarely attacked when visiting other groups. We showed that helpers are able to strategically emigrate and join another group as a helper and suggest that visiting behaviour may be a means to prepare between-group dispersal. The possibility to disperse to other groups provides an alternative to the two main options of subordinates in cooperative breeders, i.e., to stay and help or to leave and reproduce independently. We suggest this additional option should have important consequences for the costs and benefits of staying versus leaving in cooperative breeders.

Group size, competition and territory quality

Our data confirm results of a previous study that large groups occupied higher quality territories with more shelters (Balshine et al., 2001). But we show that these territories were also more densely occupied, which is reflected by an increase in the competition index in larger groups. Group augmentation effects have been suggested to explain increased survival or reproduction in larger groups (Kokko et al., 2001). In larger groups of *N. pulcher* individuals spend more time feeding, breeders have a lower workload and increased reproductive success (Balshine et al., 2001), survival is higher (Heg et al., 2004a), and larger groups are more stable between years (Heg et al., 2005), likely because of enhanced safety benefits from predators (Taborsky, 1984; Balshine et al., 2001). Consequently, group augmentation benefits may explain the positive relationship between group size and competition index: they may compensate for the costs of increased competition between helpers in larger groups and reduce the need for shelter for each single helper.

Helper visits of other groups

Two non-exclusive hypotheses may explain why helpers regularly visited neighbouring groups. First, helpers may prepare potential between-group dispersal. By visiting they acquire public information (Valone & Giraldeau, 1993) about the benefits of dispersing into another group, i.e., expected fitness in a subordinate role or the likelihood of acquiring a breeding position in the target group (i.e., 'prospecting behaviour', see Reed et al., 1999; Doligez et al., 2002). However, although helpers who had longer queues in their home group engaged more in visiting behaviour, we did not find evidence for preferential visits to groups with expected higher fitness in case of between group dispersal (i.e., higher number of shelters, shorter queue length or lower competition index of the visited group). Helpers visited groups more often, but less long when they contained more large helpers. High quality territories might be more attractive to visit but at the same time might contain more large helpers. On the other hand, increased competition for high quality territories might cause shorter visiting durations. Further studies are needed to clarify a potential relationship between visiting behaviour and group or territory quality. Second, helpers may use the shelters in other territories as refuge from predators. This second hypothesis is supported by their behaviour after experimental disturbance in the home territory: when perceived risk was high helpers readily took refuge in other groups' territories and spent about twice as much time in other groups territories, compared to the control observations of the same helpers.

Regular and prolonged visits of other groups may be an indication of bad conditions for a helper at home, e.g. due to competition with other helpers or a threat of eviction by the dominants, resulting in the helper watching out for an alternative group to join. As helpers visiting other groups were not subjected to higher aggression levels in their home group compared to helpers that did not perform visits, our data do not support this explanation. However, adverse conditions that might result from punishment for example may be difficult to detect (Bergmüller & Taborsky, 2005).

Helpers visiting other groups showed more submissive behaviour in their home territory than helpers that did not engage in visits. This is consistent with results of previous studies that showed that helpers which were separated from the group (but still within their home territory) increased their submissive behaviour when able to interact with their group again

(Bergmüller & Taborsky, 2005). Similarly, helpers that spent time away from their home territory either voluntarily (Bergmüller et al., 2005) or forced by manipulation (Balshine-Earn et al., 1998) increased their submissive behaviour upon return. These observations suggest that leaving the group to visit other groups may jeopardize the helper's group membership. Helpers that leave the group appear to incur costs and might risk punishment by other group members if they do not sufficiently signal their willingness to act cooperatively upon return (Balshine-Earn et al., 1998).

Helper dispersal to other groups

In cooperative breeders, groups containing unrelated individuals due to immigration of subordinates are widespread. In some bird species unrelated helpers reproduce in the new group (Sherman, 1995; Whittingham et al., 1997; Li & Brown, 2000; Richardson et al., 2003), while in others subordinates do not participate in reproduction (Reyer, 1980; Sherley, 1990; Haig et al., 1994), or do not help (Gardner et al., 2003). Between group migration of subordinates is also known from many mammals (Rood, 1987; Solomon & French, 1997), and invertebrates (Field et al., 1999). In dwarf mongooses (*Helogale parvula*), between-group dispersal of helpers was shown to improve their position in the queue for a breeding vacancy and, in addition, it is consistent with inbreeding avoidance (Rood, 1987). Also in Seychelles warblers (*Acrocephalus sechellensis*), subordinate males are able to reproduce in the new groups and between-group dispersal of male helpers may be explained by inbreeding avoidance (Richardson et al., 2003). Despite several reports of between group-dispersal in cooperatively breeding species, the significance of strategic between-group migration of helpers (and strategic helper recruitment by dominants) for group dynamics and regulation of cooperative behaviour is as jet largely unresolved.

Although we have observed that helpers in *N. pulcher* frequently scan their environment and visit nearby groups, actual strategic dispersal was rare. This corresponds to the low estimates of between-group dispersal provided by genetic markers and long-term observations (Stiver et al., 2004; Dierkes et al., 2005). The opportunities to disperse into another group may be limited in *N. pulcher* and yield a low benefit/cost ratio. However, for single individuals, strategic between-group dispersal might still be a better option than dispersal to a vacant territory as experiments in the field showed that helpers

do not readily occupy a vacant territory (Heg, Bacher, Brouwer & Taborsky, unpubl.) and single breeding pairs are rarely observed under natural conditions (Taborsky & Limberger, 1981; Balshine et al., 2001).

Whether dispersal is 'voluntary' or 'forced' should affect helper fitness in opposite directions. With voluntary dispersal we expect an increase in helper fitness, whereas with forced dispersal, helper fitness should on average decrease. Expelled individuals lose the benefits of access to shelter and group membership and should quickly take refuge in another group. In contrast, voluntary dispersal of subordinates appears to be a gradual process starting with visits to nearby groups, eventually leading to permanent membership in another group which might provide better conditions to the helper. As helpers that were induced to disperse migrated further away from their home territory than those that dispersed or attempted to do so voluntarily, our data suggest that visits and the resulting familiarity with nearby groups facilitate successful strategic between-group dispersal. However, due to our small sample size, we cannot compare the fitness consequences of voluntary or enforced dispersal on helper fitness. Furthermore, since many aspects of group composition are positively correlated (e.g., group size, territory size, breeder male size, breeder female size, largest helper size) (Balshine et al., 2001; Heg et al., 2005), further experiments should test whether helpers adjust their visiting and dispersal behaviour according to the expectations generated by our results.

Social networks, extended safe havens and biological markets

Helpers spent more than five percent of their time visiting other groups' territories, where they often seemed to be tolerated. This is surprising, as previous lab experiments have shown that group members individually recognise each other (Hert, 1985; Balshine-Earn & Lotem, 1998) and aggressively defend their territory against unfamiliar conspecific intruders (Taborsky, 1985; Bergmüller & Taborsky, 2005). In contrast, our field observations showed that aggression levels received in other groups' territories did not significantly differ from those received at home, and visiting helpers were in general clearly not treated as intruders. Thus, visits of helpers may serve to build up a social network with neighbouring groups (McGregor, 1993; Croft et al., 2004). As a result of familiarity, mutual access to other groups' territories provides 'extended safe havens', i.e., refuges from predators outside

the home territory, which has been shown to be of critical importance (Heg et al., 2004a).

As we observed that helpers can indeed strategically migrate to other groups, and as dominants may gain fitness by accepting additional helpers (Taborsky, 1984; Brouwer et al., 2005), helpers might trade their helping contribution for being accepted in a territory that provides beneficial conditions. This is expected in a biological market scenario, where demand and supply determine the values of commodities exchanged (Noë & Hammerstein, 1995; Noë, 2001). Several lines of evidence suggest that biological market principles may at least partly explain visiting behaviour and between group dispersal in *N. pulcher*: the low level of breeder aggression towards intruding helpers, the observation of subordinate between-group dispersal, and the regular occurrence of groups with unrelated helpers and breeders (Stiver et al., 2004; Dierkes et al., 2005). We suggest that biological market theory can be invoked in all cooperatively breeding species where individuals may migrate between groups.

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References

Alberts, S.C. & Altmann, J. (1995). Balancing costs and opportunities – dipsersal in male baboons. — Am. Nat. 145: 279-306.

Baglione, V., Marcos, J.M., Canestrari, D. & Ekman, J. (2002). Direct fitness benefits of group living in a complex cooperative society of carrion crows, *Corvus corone corone*. — Anim. Behav. 64: 887-893.

Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M. & Werner, N. (2001). Correlates of group size in a cooperatively breeding cichlid fish. — Behav. Ecol. Sociobiol. 50: 134-140.

Balshine-Earn, S. & Lotem, A. (1998). Individual recognition in a cooperatively breeding cichlid: evidence from video playback experiments. — Behaviour 135: 369-386.

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

Bergmüller, R., Heg, D. & Taborsky, M. (2005). Helpers in a cooperatively breeding cichlid fish stay and pay, but choose to leave when independent breeding options are available. — Proc. R. Soc. Lond. B 272: 325-331.

Bergmüller, R. & Taborsky, M. (2005). Experimental manipulation of helping in a cooperative breeder: helpers 'pay-to-stay' by pre-emptive appeasement. — Anim. Behav. 69: 19-28.

Brouwer, L., Heg, D. & Taborsky, M. (2005). Experimental evidence for helper effects in a cooperatively breeding cichlid. — Behav. Ecol. 16: 667-673.

Clutton-Brock, T.H. (1998). Reproductive skew, concessions and limited control. — Trends Ecol. Evol. 13: 288-292.

Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D. & Brotherton, P.N.M. (1999). Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. — J. Anim. Ecol. 68: 672-683.

Crawley, M.J. (2002). Statistical computing. An introduction to data analysis using S-Plus. — Chichester, Wiley.

Creel, S.R. & Waser, P.M. (1994). Inclusive fitness and reproductive success in dwarf mongooses. — Behav. Ecol. 5: 339-348.

Croft, D.P., Krause, J. & James, R. (2004). Social networks in the guppy (*Poecilia reticulata*). — Proc. R. Soc. Lond. B (Supplement) 271: S516-S519.

Dierkes, P., Heg, D., Taborsky, M., Skubic, E. & Achmann, R. (2005). Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. — Ecology Letters 8: 968-975.

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

Dingemanse, N.J., Both, C., Van Noordwijk, A.J., Rutten, A.L. & Drent, P.J. (2003). Natal dispersal and personalities in great tits (*Parus major*). — Proc. R. Soc. Lond. B 270: 741-747.

Doligez, B., Danchin, E. & Clobert, J. (2002). Public information and breeding habitat selection in a wild bird population. — Science 297: 1168-1170.

East, M.L. & Hofer, H. (2001). Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. — Behav. Ecol. 12: 558-568.

Emlen, S.T. (1997). Predicting family dynamics in social vertebrates. — In: Behavioural ecology. An evolutionary approach (Krebs, J.R. & Davies, N.B., eds). Blackwell Science, Oxford, p. 228-253.

Ens, B.J., Weissing, F.J. & Drent, R.H. (1995). The despotic distribution and deferred maturity – 2 sides of the same coin. — Am. Nat. 146: 625-650.

Fedigan, L.M. & Jack, K.M. (2004). The demographic and reproductive context of male replacements in *Cebus capucinus*. — Behaviour 141: 755-775.

Field, J., Shreeves, G. & Sumner, S. (1999). Group size, queuing and helping decisions in facultatively eusocial hover wasps. — Behav. Ecol. Sociobiol. 45: 378-385.

Gardner, J.L., Magrath, R.D. & Kokko, H. (2003). Stepping stones of life: natal dispersal in the group-living but noncooperative speckled warbler. — Anim. Behav. 64: 1-10.

Gaston, A.J. (1978). The evolution of group territorial behavior and cooperative breeding. — Am. Nat. 112: 1091-1100.

Grantner, A. & Taborsky, M. (1998). The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: Cichlidae). — J. Comp. Physiol. B 168: 427-433.

Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. — Anim. Behav. 28: 1140-1162.

Griffin, A.S. & West, S.A. (2002). Kin selection: fact and fiction. — Trends Ecol. Evol. 17: 15-21.

Haig, S., Walters, J.R. & Plissner, J.H. (1994). Genetic evidence for monogamy in the cooperatively breeding red-cokaded woodpecker. — Behav. Ecol. Sociobiol. 34: 295-303.

Hamilton, I.M. & Taborsky, M. (2005). Unrelated helpers will not fully compensate for costs imposed on breeders when they pay to stay. — Proc. R. Soc. Lond. B 272: 445-454.

Heg, D., Bachar, Z., Brouwer, L. & Taborsky, M. (2004a). Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. — Proc. R. Soc. Lond. B 271: 2367-2374.

Heg, D., Bender, N. & Hamilton, I.M. (2004b). Strategic growth decisions in helper cichlids. — Proc. R. Soc. Lond. B (Supplement) 271: 505-508.

Heg, D., Brouwer, L., Bachar, Z. & Taborsky, M. (2005). Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. — Behaviour 142: 1615-1641.

Hert, E. (1985). Individual recognition of helpers by the breeders in the cichlid fish *Lamprologus brichardi* (Poll, 1974). — Z. Tierpsychol. 68: 313-325.

Jack, K.M. & Fedigan, L. (2004). Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 2: patterns and causes of secondary dispersal. — Anim. Behav. 67: 771-782.

Johnson, M.L. & Gaines, M.S. (1990). Evolution of dispersal: Theoretical models and empirical tests using birds and mammals. — Ann. Rev. Ecol. Syst. 21: 449-480.

Johnstone, R.A. (2000). Models of reproductive skew: A review and synthesis. — Ethology 106: 5-26.

Kalas, K. (1975). Zur Ethologie von *Lamprologus brichardi* (Pisces, Cichlidae). — Univ. Giessen.

Kokko, H. & Ekman, J. (2002). Delayed dispersal as a route to breeding: Territorial inheritance, safe havens, and ecological constraints. — Am. Nat. 160: 468-484.

Kokko, H. & Johnstone, R.A. (1999). Social queuing in animal societies: a dynamic model of reproductive skew. — Proc. R. Soc. Lond. B 266: 571-578.

Kokko, H., Johnstone, R.A. & Clutton-Brock, T.H. (2001). The evolution of cooperative breeding through group augmentation. — Proc. R. Soc. Lond. B 268: 187-196.

Kokko, H., Johnstone, R.A. & Wright, J. (2002). The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? — Behav. Ecol. 13: 291-300.

Kokko, H. & Lundberg, P. (2001). Dispersal, migration, and offspring retention in saturated habitats. — Am. Nat. 157: 188-202.

Komdeur, J. (1992). Importance of habitat saturation and territory quality for evolution of cooperative breeding in the seychelles warbler. — Nature 358: 493-495.

Li, S.H. & Brown, J.L. (2000). High frequency of extrapair fertilization in a plural breeding bird, the Mexican jay, revealed by DNA microsatellites. — Anim. Behav. 60: 867-877.

McGregor, P.K. (1993). Signalling in territorial systems: A context for individual identification, ranging and eavesdropping. — Phil. Trans. R. Soc. Lond. B 340: 237-244.

Noë, R. (2001). Biological markets: partner choice as the driving force behind the evolution of mutualisms. — In: Economics in nature (Noë, R., van Hooff, J.A.R.A.M. & Hammerstein, P., eds). Cambridge University Press, Cambridge, p. 93-118.

Noë, R. & Hammerstein, P. (1995). Biological markets. — Trends Ecol. Evol. 10: 336-339.

Pusey, A. & Wolf, M. (1996). Inbreeding avoidance in animals. — Trends Ecol. Evol. 11: 201-206.

Pusey, A.E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. — Trends Ecol. Evol. 2: 295-299.

Reed, J.M., Boulinier, T., Danchin, E. & Oring, L.W. (1999). Informed dispersal: prospecting by birds for breeding sites. — Curr. Ornithol. 15: 189-259.

Reyer, H.U. (1980). Flexible helper structure as an ecological adaptation in the pied kingfisher, *Cerle rudis rudis* L. — Behav. Ecol. Sociobiol. 6: 219-227.

Richardson, D.S., Burke, T. & Komdeur, J. (2003). Sex-specific association learning cues and inclusive fitness benefits in the Seychelles warbler. — J. Evol. Biol. 16: 854-861.

Rood, J.P. (1987). Dispersal and intergroup transfer in the dwarf mongoose. — In: Mammalian dispersal patterns. The effects of social structure on population genetics (Chepko-Sade, B.D. & Halpin, Z.T., eds). University of Chicago Press, Chicago, p. 85-103.

Sapolsky, R.M. (1996). Why should an aged male baboon ever transfer troops? — Am. J. Primatol. 39: 149-157.

Schradin, C. & Lamprecht, J. (2002). Causes of female emigration in the group-living cichlid fish *Neolamprologus multifasciatus*. — Ethology 108: 237-248.

Sherley, G.H. (1990). Co-operative breeding in the riflemen (*Acanthisitta cloris*): benefits to parents, offspring and helpers. — Behaviour 109: 1-22.

Sherman, P.W. (1995). Social organisation of cooperatively polyandrous white-winged trumpeters (*Psophia leucoptera*) in Peru. — Auk 112: 296-309.

Skubic, E., Taborsky, M., McNamara, J.M. & Houston, A.I. (2004). When to parasitize? A dynamic optimization model of reproductive strategies in a cooperative breeder. — J. theor. Biol. 227: 487-501.

Solomon, N.G. & French, J.A. (1997). Cooperative breeding in mammals. — Cambridge University Press, Cambridge.

Stiver, K.A., Dierkes, P., Taborsky, M. & Balshine, S. (2004). Dispersal patterns and status change in a co-operatively breeding fish *Neolamprologus pulcher*: evidence from microsatellite analyses and behavioural observations. — J. Fish Biol. 65: 91-105.

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

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

Taborsky, M. & Grantner, A. (1998). Behavioural time-energy budgets of cooperatively breeding *Neolamprologus pulcher* (Pisces: Cichlidae). — Anim. Behav. 56: 1375-1382.

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

Valone, T.J. & Giraldeau, L.A. (1993). Patch estimation by group foragers – What information is used. — Anim. Behav. 45: 721-728.

Werner, N.Y., Balshine-Earn, S., Leach, B. & Lotem, A. (2004). Helping opportunities and space segregation among helpers in cooperatively breeding cichlids. — Behav. Ecol. 14: 749-756.

Whittingham, L.A., Dunn, P.O. & Magrath, R.D. (1997). Relatedness, polyandry and extra-group paternity in the cooperatively-breeding white-browed scrubwren (*Sericornis frontalis*). — Behav. Ecol. Sociobiol. 40: 261-270.