Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish

Sigal Balshine-Earn, Francis C. Neat, Hannah Reid, and Michael Taborsky
Konrad Lorenz Institute for Comparative Ethology (KLIVV), Savoyenstrasse 1a, A-1160, Vienna, Austria

Several hypotheses aim to explain the evolution of helping behavior, but conclusive experimental support for evaluating the relative importance of individual hypotheses is still lacking. We report on two field experiments conducted to test the "territory inheritance" and "pay-to-stay" hypotheses in the cooperatively breeding cichlid fish *Neolamprologus pulcher*. The territory inheritance hypothesis was tested by removing one parent, which created breeding vacancies. In 39% of cases, same-sex helpers took over the breeding spot; in 44% of cases helpers continued helping new breeders, and 17% were evicted by new breeders. Helpers that were closely size matched to the removed breeder had a better chance of gaining the breeding spot. Male helpers tended to continue helping after a takeover more often than females. The pay-to-stay hypothesis was tested by temporarily removing helpers. Whereas breeders did not respond aggressively to removals, other group members attacked the removed helpers on their return, and 29% were eventually evicted. The returning helpers assisted more by increasing their rate of territory maintenance and defense and visiting the brood chamber more frequently. Size and sex of removed helpers did not explain the observed aggressive reactions of other group members. Thus, our results support both hypotheses: *N. pulcher* needs to pay with help to be allowed to remain protected in the family group, and there they may inherit the natal territory. *N. pulcher* helpers gain direct benefits from helping behavior. *Key words:* cichlids, cooperative breeding, helping behavior, *Neolamprologus pulcher*, territory inheritance. *[Behav Ecol 9:432–438 (1998)]*

In a variety of taxa, from insects to mammals, individuals forgo opportunities to reproduce and help others to breed (Bourke, 1997; Brown, 1987; Riedman, 1982; Stacey and Koenig, 1990; Taborsky, 1994). This puzzling behavior has stimulated theoretical investigations (Brown and Pimm, 1985; Hamilton, 1964; Jamieson, 1989; Trivers, 1971; Zahavi, 1976) and two decades of long-term empirical work on animal cooperative breeding (see Emlen, 1991; Solomon and French, 1997; Stacey and Koenig, 1990, for reviews). Studies of these social systems have concentrated on two related questions: why do the helpers remain on the natal territory? and why do they help?

A number of studies have successfully provided an answer to the first question by showing that in many cooperative breeders, helpers are prevented from breeding or dispersing by particular environmental factors (Komdeur, 1992; Pruett-Jones and Lewis, 1990). However, the question of why helpers help remains a hotly debated issue (reviewed by Emlen, 1994; Heinsohn et al., 1990).

Helping behavior has fitness costs (Heinsohn and Cockburn, 1994), and therefore much effort has been expended to explain the benefits of helping behavior. Many studies have sought to understand the selective advantages to helpers in terms of kin selection (indirect benefits; Hamilton, 1964), but the existence of unrelated helpers in many cooperatively breeding species indicates that kin selection cannot be the only explanation for helping behavior (Brown, 1987; Creel and Waser, 1994; Reyer, 1980; Rood, 1978, 1990). It has therefore been suggested that helpers may also gain direct benefits

from helping behavior. Helpers may benefit by (1) receiving reciprocated help in the future (Ligon and Ligon, 1978; Trivers, 1971); (2) gaining protection and feeding benefits in the established territory (Gaston, 1978; Taborsky, 1984, 1985); (3) gaining parental experience (Brown, 1987; Komdeur, 1996; Lawton and Guindon, 1981); (4) increasing the probability of their survival through group augmentation (Taborsky, 1984; Brown, 1987); and (5) increasing the probability of mate or territory acquisition (Reyer, 1980; Woolfenden and Fitzpatrick, 1984).

Correlations from field data support several of the hypotheses mentioned above—e.g., kin selection (Brown, 1987; Emlen and Wrege, 1988; Taborsky, 1984), parental experience (Rowley and Russell, 1990); territory inheritance (Mech, 1970; Woolfenden and Fitzpatrick, 1978, 1984), and mate acquisition (Clarke, 1984, 1989; Reyer, 1980, 1984, 1986). In most species, we have yet to determine the relative importance of each influence for explaining the evolution of helping behavior. Furthermore, it is likely that several benefits accumulate and that these may be of different relative importance in different species. Moreover, the potential benefits gained by helpers may operate together; e.g., when an individual provides help it gains parental experience, assists its group and creates more relatives. Although each hypothesis proposes a different mechanism for the evolution of helping behavior, each predicts similar outcomes (e.g., an active helper that eventually obtains breeding status can be viewed as evidence for more than one hypothesis). Experiments aimed at testing specific aspects of helping behavior are the only way to tease the hypotheses apart and assess the relative merit of ideas based on unmanipulated field observations (see Taborsky, 1984, 1985).

Previously, the main targets of research on cooperative breeding have been birds and mammals, which are relatively difficult to manipulate experimentally. However, the cooperatively breeding cichlid fish *Neolamprologus pulcher* is small,

easily caught, fast growing (range of sexually mature fish 3.5–8 cm), and responds well to experimental manipulations. Therefore it is an ideal species to test which factors select for helping behavior and drive its evolution.

N. pulcher, sometimes called *Neolamprologus brichardi* is an endemic fish in Lake Tanganyika, Zambia, that inhabits small territories along the rocky shores from 3 to 45 m depth (Taborsky and Limberger, 1981). (We believe *Neolamprologus pulcher* and *N. brichardi* are one species and discuss this issue in detail elsewhere.) Breeders in this species are assisted by "helpers" in rearing young. Around the full moon, the female lays batches of eggs within a shelter (or brood chamber), and the male fertilizes them. The eggs hatch after 3–4 days, but the larvae remain in the brood chamber for another 8–9 days. The eggs and larvae are tended in the brood chamber, which also serves as the principal shelter site for the family group. Most free-swimming fry emerge around the new moon (personal observations). Besides the breeders, helpers (usually born in the territory) will contribute by sharing in all duties of brood care, territory defense, and maintenance. Helpers defend the territory by attacking potential space competitors and predators. They maintain the territory by removing particles or snails and by digging sand and debris away from the breeding shelter. They also join in direct brood care by cleaning and fanning eggs and larvae and defend the free-swimming fry from predators (Taborsky and Limberger, 1981).

In this study we had two principal aims. First, we wanted to determine whether helpers helped to be in close proximity when breeding vacancies became available in their own natal territories. We tested this "territory inheritance" hypothesis by removing breeders from territories that contained large helpers and then monitored whether these helpers took over the available breeding slot. Second, we sought to establish whether helpers help in return for being permitted to stay in their territory, which provides shelter and hence protection from predators. We tested this "pay-to-stay" hypothesis by manipulating helping effort through temporary removals of specific individuals and then monitoring their behavior and the behavior of breeders and other group members toward them before and after the removals.

METHODS

We studied 74 *N. pulcher* families in 12 colonies in Lake Tanganyika, Zambia. Eleven colonies (7–9 m depth, approximately 175 m from the shore) were located in Kasakalawe Bay (west of Mpulungu); one (3 m depth, 5 m from the shore) was at Mutondwe Island (east of Mpulungu). A colony consists of a group of clustered territories that share common boundaries. Our study was conducted from 17 December 1996 to 8 April 1997. Observations were made by scuba diving.

Frequencies of all helping behaviors per watch (brood care: number of visits to and duration in the brood chamber; territory maintenance: digging and carrying; and defense: attacks on neighbors and predators) were recorded. As it was not possible to observe behavior in the brood chamber, we measured the duration and frequency of visits to the brood chamber and ascribed these as brood care (see Coeckelberghs, 1974, for an ethogram of the full set of behaviors recorded.) We allowed for a 5-min habituation period before each 15-min focal watch.

Fish were captured by guiding them into transparent plexiglass tubes with hand nets. Fish were measured (standard length and depth, cm), sexed, and individually marked by fin clipping and injection of nontoxic acrylic paints (3 colors) into 1–3 scale pouches in 16 possible locations on the body (Dierkes, 1996). Fish were then released back into their territory.

Territory inheritance hypothesis

Of the 74 families studied, 18 were selected that contained a large sexually mature helper about the size of the male (n = 9) or the female breeder (n = 9). The mean size difference between the 18 selected pairs of helpers and breeders was 0.50 cm standard length (SL) ± 0.13 (0.40 cm = median). Each of the breeding male, female, and focal helper in these families were observed for 15-min focal watches twice a day for 2 days. Then the breeding male was removed in the nine families with a large male helper and the female breeder removed in the nine families with a large female helper. The focal helper was observed for another two 15-min focal watches, the first and second day after the breeder removals, once in the afternoon and once in the morning (a total of four watches). We recorded all helping behaviors as well as breeding male-female and breeder-helper interactions before and after the removals. This experiment was conducted 24–31 March and was timed to coincide with the peak spawning activity that occurs following the full moon (24 March).

Pay-to-stay hypothesis

On average families contained five helpers. Out of the 74 families, 17 families were selected because they had two sexually mature (>3.5 cm) helpers that could be matched for size and sex. These helpers' mean size was 4.7 cm (3.6–5.7 cm). Overall, helper number in these particular families ranged from 2 to 13. In each family, one of the two matched helpers was randomly chosen as the control, the second as the experimental. The experimental helper was observed for 15 min before the removal and then removed from its family for 4–6 h. During the removal it was placed in a mesh cage (30 cm × 20 cm × 20 cm) several meters away from the colony and out of sight from the other family members.

Directly before returning the experimental helper, the control helper was observed for 15 min. We observed the control helper to ensure that any changes in behaviors were a result of the removal and not simply caused by a numerical change in the group or a temporal fluctuation in activity patterns. The experimental helper was then returned and observed again for 15 min, as was the control helper. The experimental fish was observed again for 15 min the next day. Therefore, each experimental family was observed for 75 min in total.

RESULTS

Territory inheritance hypothesis

Seven out of 18 helpers (39%) took over the vacant breeding spot and showed behavior typical of breeders. The male removals resulted in three territory takeovers by male helpers, whereas six male helpers remained as helpers with new males. In the families where breeding females were removed, four female helpers took over the breeding vacancy, two helpers continued helping for a new female, and three female helpers were evicted by new females. In all but one group, takeovers occurred before the next observation period.

In this one group (mentioned above) initially the female helper behaved as a breeding female around a secondary shelter, courting and being courted by the breeding male and co-defending this shelter. However, the breeding male also courted a new female in the primary shelter (brood chamber). By the next day, the ex-helper (injured by the new female) moved out of the natal territory. Although this is only a single example and we did not observe the takeover, it is possible that all disappearances followed failed takeover attempts. We plan to investigate this idea in future work.

There were no sex differences in the likelihood of a take-
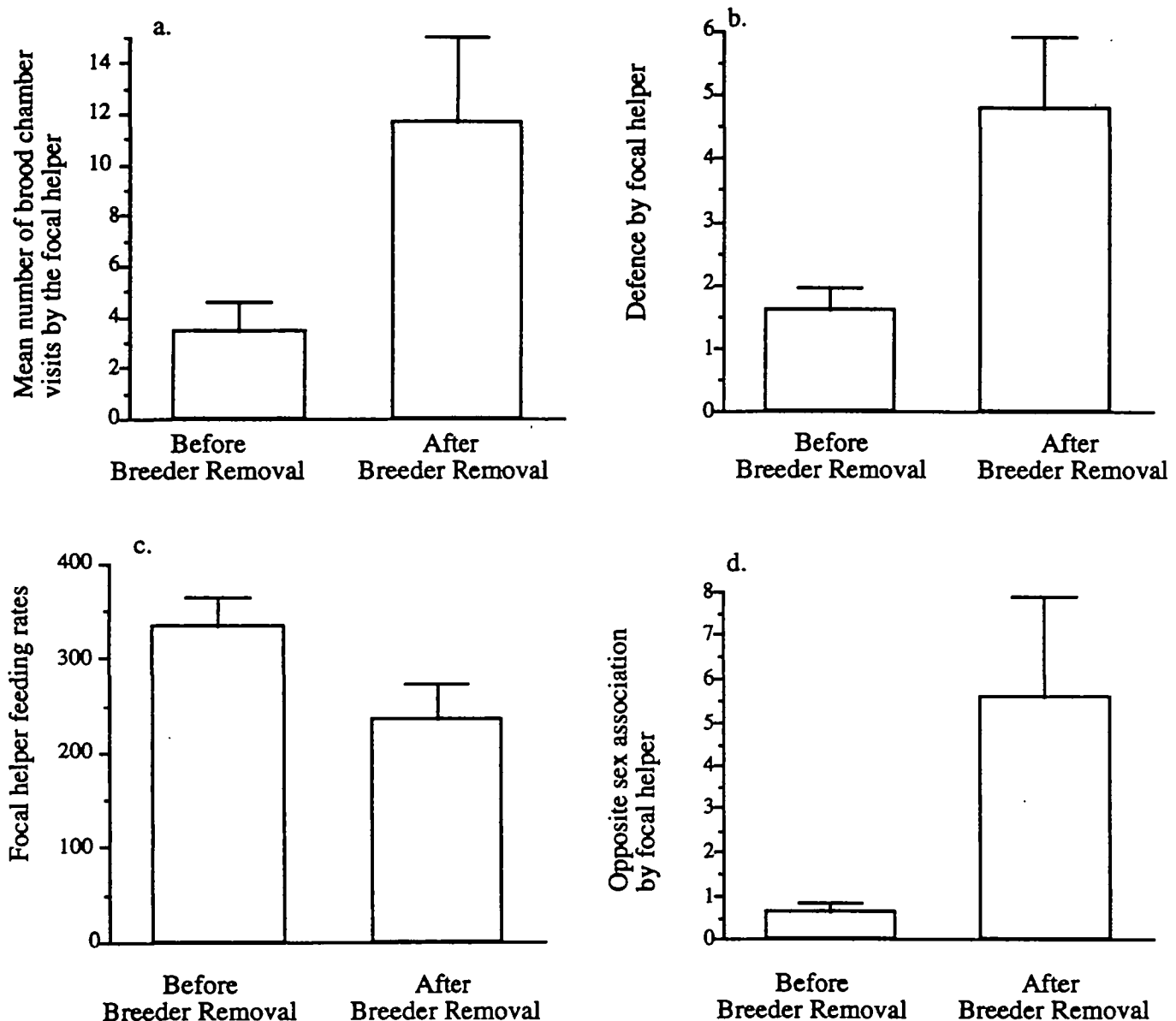
Figure 1
The frequency of brood-care behaviors performed by focal helpers before and after breeders were removed. The mean frequency of (a) brood chamber visits, (b) defense, (c) feeding rates, and (d) opposite-sex associations ($n = 18$ helpers). Bars are standard errors.

over (Fisher's Exact test, $p = .33$), nor of being evicted (Fisher's Exact test, $p = .10$). However, there was a tendency for more males to stay on their natal territory as helpers (Fisher's Exact test, $p = .07$).

Ex-helpers who took over behaved as dominant breeders. Comparison between before and after the breeder removals revealed that after breeder removal, all focal helpers (both sexes combined) increased: the number of visits to the brood chamber ($n = 18$, $z = 2.0$, $p = .05$), rates of defense ($n = 18$, $z = 2.3$, $p = .03$), and associations with the opposite sex (non-removed) breeder ($n = 18$, $z = 2.9$, $p = .004$) increased, but feeding decreased ($n = 18$, $z = 2.3$, $p = .02$). Associations included courtship displays (parallel swimming, shakes, quivers, etc.) as well as joint visits to the brood chamber. These former helpers also received more submissive displays after the removal ($n = 18$, $z = 2.7$, $p = .006$; Figure 1).

In general, breeders were larger than helpers. Focal helpers closest in body size (standard length) to breeder size were

more likely to take over [Kruskal Wallis test, H (corrected for ties) $= 7.5$, $p = .02$; Figure 2]. Multiple comparisons between treatments (following the Kruskal Wallis test; Siegel and Castellan, 1988) indicated that takeover helpers were more closely matched in body size to breeders when compared to helpers that remained as helpers for new breeders or helpers that were evicted when a nongroup member took over (critical value $= 6.6$, $|\bar{R}_{TO} - \bar{R}_{SH}| = 7.1$, critical value $= 8.7$, $|\bar{R}_{TO} - \bar{R}_{EH}| = 2.8$, critical value $= 10.6$, $|\bar{R}_{EH} - \bar{R}_{SH}| = 4.3$).

Pay-to-stay hypothesis

Breeders' and other group members' responses to the removals
Upon release, helpers typically swam into the center of the territory and within 1 min were detected by other group members. We defined detection as any group members who oriented and approached (within 10 cm) the returned help-
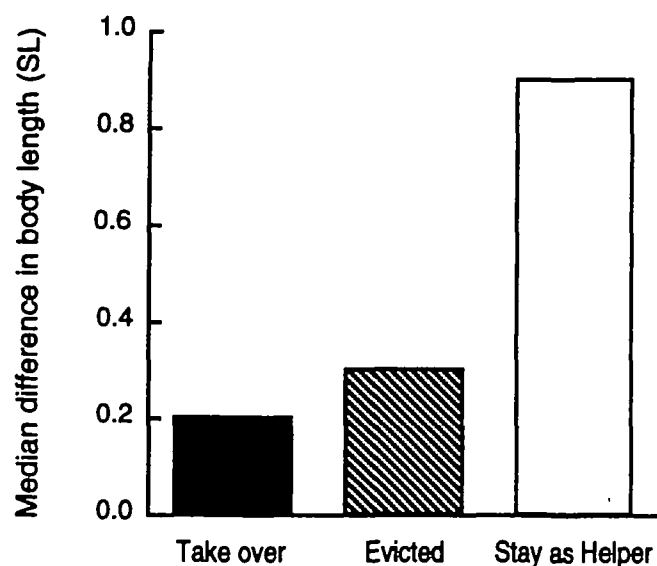
Figure 2
The median difference in body length in centimeters (standard length) between the removed breeders and the focal helper in families where the helper took over (solid bar), was evicted (striped bar), or stayed on as a helper for a new breeder (open bar).

ers. They were either passively accepted back or were subjected to harassment. We examined the reactions of the breeders and other group members separately. In 3 cases out of 17, breeders attacked the returned individuals, but the other breeders ignored the returning helpers. We compared the number of attacks removed helpers received from breeders before and after the removals and found no significant difference [Wilcoxon matched-pairs test, n = 17, z (tied) = 1.2, p = .24]. We did not detect any initial behavioral differences between experimental helpers that were ignored and those that were attacked.

In contrast, nine returning helpers were aggressively attacked (bitten, rammed, and chased) by the other helpers in their group. We compared number of attacks by other helpers on the removed helpers before and after the removal and found that the number of attacks significantly increased [Wilcoxon test (all aggressive behaviors pooled), n = 17, z (tied) = 2.0, p = .04]. The experimental helpers typically responded to this aggression with increased subordinate displays, which usually appease aggression [Wilcoxon test, n = 17, z (tied) = 3.2, p = .002]. In addition, returned helpers also increased their rates of help: they performed more defense behaviors against predators and space competitors [n = 17, z (tied) = 2.5, p = .01], tended to spend more time maintaining the territory [n = 17, z (tied) = 1.7, p = .08], visited the brood chamber more frequently [n = 17, z (tied) = 2.6, p = .01], and spent more time in the brood chamber [n = 17, z (tied) = 2.5, p = .01; Figure 3].

No differences in aggressive reactions (breeders and other helpers) were found between the experimental helpers before the removals versus the control matched helpers after the removals [breeders' responses: n = 17, z (tied) = 1.0, p = .34; other group members: n = 17, z (tied) = 0.6, p = .58]. As mentioned above, these control helpers were used to ensure that any changes in behaviors were not simply caused by a numerical change in the group or a temporal fluctuation in activity patterns. For example, the control helpers visited the brood chamber more frequently than the experimental helpers before the removals [Wilcoxon test, n = 17, z (tied) =

Table 1
The relative change in aggressive and helping behaviors shown to and by males and females (expressed as frequency of behaviors after removal minus frequency before the removal)

	Males (n=8)	Females (n=9)	z (tied)	p
Breeder aggression (bites, chases, rams, mouth fights and threat displays)	0.5	0	−0.9	0.40
Other group members aggression	0	0	−1.0	0.34
Defense behaviors	2	5	−1.2	0.23
Territory maintenance behaviors	0	0	−0.3	0.76
Time (s) in brood chamber	20	61	−1.2	0.23
No. visits to brood chamber	3	9	−2.5	0.02

Median values are presented; Mann-Whitney tests were used.

2.0, p = .04]. However, control helpers were sampled later in the day, and this probably accounts for their higher visitation rates. In a separate study, we found that, on average, helpers visited the brood chamber for 65 s per 15 min between 0600 and 1200 h and for 192 s between 1200 and 1800 h [Wilcoxon signed-ranks test, n = 65, z (tied) = 2.6, p = .01]. No differences were found in the frequency of other helping behaviors between experimental and controls [territory defense: n = 17, z (tied) = 0.3, p = .78; territory maintenance: n = 17, z (tied) = 0.5, p = .59; time in brood chamber: n = 17, z (tied) = 0.8, p = .44].

Evictions
One day after the removals, 5 of the 17 removed helpers had disappeared. They were not seen again on their natal territories or anywhere else. Size and sex did not explain the evictions, but the sample size is small. We observed these families for nearly 3 months before performing the removal experiments. Unmanipulated helpers were never observed to be forcibly evicted by breeders or other group members. Helper disappearances were infrequently recorded, but these were al-

Table 2
The relative change in aggressive and helping behaviors shown to and by large versus small helpers (expressed as frequency of behaviors after removal minus frequency before the removal)

	Small helpers (n=10)	Large helpers (n=7)	z (tied)	p
Breeder aggression	0.5	0	−0.8	0.42
Other group members aggression	0	0	−0.8	0.44
Defense behaviors	3	5	−0.8	0.41
Territory maintenance behaviors	0	0	−0.4	0.72
Time (s) in brood chamber	39	87	−0.8	0.43
No. visits to brood chamber	5.5	5	−0.1	0.92

Median values are presented; Mann-Whitney tests were used.
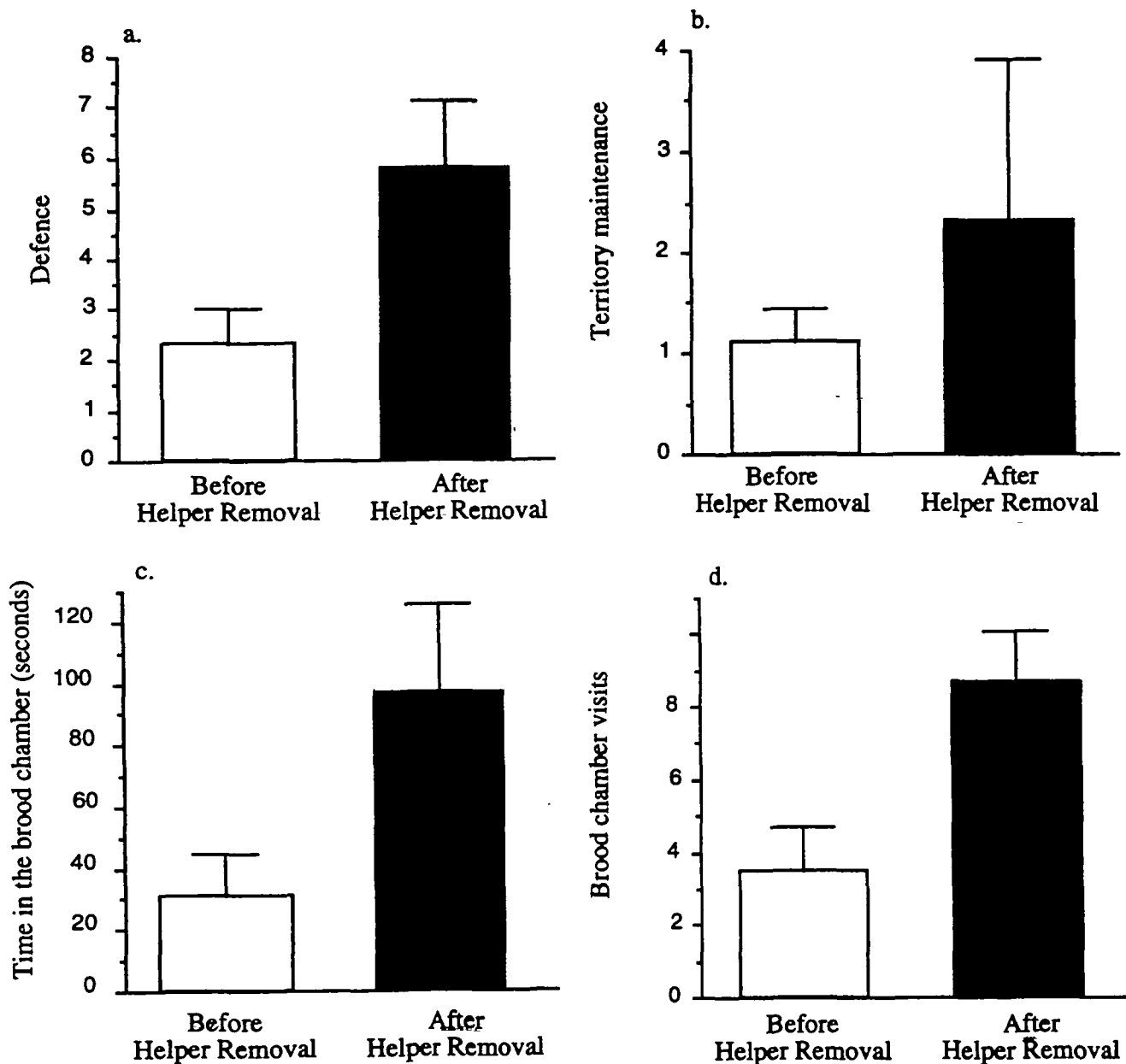
Figure 3
The mean frequency of helping behaviors performed by the experimental helper before and after it was removed (a) defense, (b) maintenance, (c) time in brood chamber, (d) number of brood chamber visits (n = 17 helper removals). Bars are standard errors.

ways associated with predation (e.g., attacks observed or scars on the body the day before disappearing) or marking. We randomly selected 17 unmanipulated families (0 evictions) and compared the probabilities of evictions with the 17 families in which we temporarily removed helpers. These unmanipulated families were marked and observed for a period of 2–3 months during which family number and composition were recorded weekly. The rate of eviction was greater than one would expect by chance in the families where helpers were removed (Fisher's Exact test, p = .02). Family size seemed to have no influence on eviction rates: three of five evictions that followed the removals occurred in families that were smaller than the average (mean = 7 individuals; 4, 6, and 6 individuals, respectively), and two evictions occurred in families that were larger than the average (10 and 13 individuals).

Sex and size

Eight of the 17 removed helpers were males and 9 were females. We examined breeder responses, other helpers responses, and helping rates of removed helpers for males and females separately and found that sex only influenced the number of brood chamber visits (Table 1). Female helpers visited the brood chamber relatively more often after the removals than did male helpers.

Although all the experimental helpers in this study were presumably sexually mature (>3.5 cm SL), we divided helpers into two size groups to check for size effects: small (3.6–4.9 cm SL individuals, n = 10) and large helpers (5–5.7 cm SL individuals, n = 7). We examined breeders responses, other group member responses, and helping rates in relation to size and found that body size did not influence these factors (Table 2).

DISCUSSION

Territory inheritance

After removal of breeders, helpers either took over (39% of cases), remained on as helpers with a new breeder (44%), or were evicted from their natal territories (17%). Male helpers were never evicted and were more likely to remain and help. Takeovers were more likely when the body size difference between helper and breeder was small. Helpers that did not take over the breeding vacancy may not have been large enough to compete with other potential breeders in the area.

In our experiment, we created breeding vacancies in the helper's own natal territories (as did Taborsky, 1984). Thus we were testing the hypothesis that helpers remain on natal territories to increase their chances of inheritance. In the first such experiment conducted on cooperatively breeding birds, Pruett-Jones and Lewis (1990) created 33 breeding vacancies for superb fairy wrens by removing male neighbors. All but two potential breeders dispersed into the created vacancies, but only when the territory contained a female. Pruett-Jones and Lewis designed their experiment to determine why helpers stay. Young, male superb fairy wrens may take over neighboring territories, and they seem to delay dispersal in response to a limited number of mates and secondarily to habitat limitation. Conversely, our experiment was designed to investigate why helpers help. Our results showed that helpers (both sexes) might help because they may gain fitness benefits by inheriting the breeding spot (both a mate and a territory).

In Zambia (southern shore of Lake Tanganyika) helpers frequently took over (7/17 cases). In contrast to our results, in the northern part of the lake (Burundi), Taborsky (1984) found that helpers never inherited the natal territory when breeding vacancies were experimentally created (0/10 cases), although helper disappearances were observed after breeder removals (Taborsky, 1982, 1984). The significant difference in takeover rates was probably a result of the environmental and demographic differences between north and south populations. In the north, the habitat was saturated (shelters are scarce) and fish live in large feeding aggregations after leaving their natal territories (Taborsky, 1984). In the south shelters abound, and feeding aggregations were never observed.

Pay to stay

N. pulcher breeders usually ignored returning helpers, whereas other helpers attacked them, and 5 out of 17 returned helpers were eventually evicted. Differences in size and sex between helpers did not account for attacks received. Helpers responded to aggression with submissive behavior and helped to a greater extent after returning to their territories.

To explain why helpers attacked removed helpers, we propose three potential explanations. First, helpers may have been attacked because they were not recognized. This is extremely unlikely for a number of reasons. (1) There is strong experimental evidence that *N. pulcher* has finely tuned visual recognition capabilities. Parents can discriminate their own helpers from other helpers of similar size (Hert, 1985). In addition, *N. pulcher* reacts appropriately to video playbacks of familiar versus unfamiliar conspecifics (Balshine-Earn and Lotem, 1998). (2) Recognition of other group members is critically important and likely in a cooperative social species. Selection should favor the ability to distinguish between the acceptable presence of helpers and unwelcome strangers. (3) Breeders largely ignored helpers, which suggests that removed helpers were recognized. Strange fish and philandering neighbors are vigorously attacked by all members of the family (personal observations). Unlike intruders, who normally flee from the attack, returned helpers attempted to stay and im-

mediately rejoined in group activities. Therefore we reject this explanation.

Second, lazy helpers may be attacked as punishment for not helping. But why should other helpers punish if breeders do not? The presence of helpers increases fecundity of female breeders (Taborsky, 1984), so breeders were expected to bear the cost (both time and energy) of punishment. Perhaps breeders only demand help when it is needed (e.g., in a laboratory experiment, previously expelled helpers were reaccepted when space competitors were introduced; Taborsky, 1985). Other helpers may have punished "lazy" helpers because each helper's presence or efforts may reduce the risks and workload (and hence increase feeding opportunities) for other helpers in the family. In another study we were able to show that feeding rates are higher in larger groups with more helpers (Balshine-Earn et al., unpublished)

Third, other helpers may have been aggressive as a result of a change in the social status and the dominance hierarchy being reestablished in the group after the removal. If there is a queue for the breeding spot, helpers may fight hard to remove another helper (potentially in front of them) from the queue. A breeding queue may explain why it pays to stay and help. We favor this explanation because it appears to be the most parsimonious; additional work is required to confirm this.

Why did returning helpers help more? Perhaps "help" signals group membership and commitment. So helping may reduce the likelihood of attack or eviction. Alternatively, helping may be a mechanism for establishing or maintaining dominance (Zahavi, 1976).

Our study is the second to date to experimentally test the pay-to-stay hypothesis in the field. Mulder and Langmore (1993) removed superb fairy wren helpers and found that only the dominant male attacked these helpers, and then only during egg incubation and chick-feeding stages. Our experiment was conducted from 15 to 24 March 1997 following new moon (when fry usually emerge), a period when fry defense should be essential. Unfortunately, only 3 of our 17 families contained newly emerged fry. In one such family the temporarily removed helper was eventually evicted. The sample of families with fry was too small to examine the aggressive response in relation to the importance of helper contributions. However, Mulder and Langmore's study and ours illustrate that the reasons for tolerating helpers may vary across species and populations (Clutton-Brock & Parker, 1995).

In conclusion, although the costs of family life have been measured in the laboratory and the field (Grantner and Taborsky, in press; Heinsohn and Cockburn, 1994; Taborsky, 1984; Taborsky and Grantner, in press), attempts to experimentally measure the potential benefits of helping under natural conditions are rare. We designed this study to separate and evaluate the relative importance of two likely factors selecting for helping behavior in *N. pulcher*. We found evidence for both pay-to-stay and territory inheritance hypotheses, and more experiments will be needed to evaluate the relative importance of each. Large helpers can inherit their natal territories, and they seem to help to remain in the safety of the group and territory. *N. pulcher* probably must help while it waits to inherit a breeding spot.

the Zambian Ministry of Agriculture, Food and Fisheries, Ruben Sha-pola, and David Ngundu for their assistance and technical support.

REFERENCES

Balshine-Earn S, Lotem A, 1998. Experimental evidence for individual recognition from video playbacks in a cooperatively breeding cich-lid (*Neolamprologus brichardi*). Behaviour 135:369–386.

Bourke AFG, 1997. Sociality and kin selection in insects. In: Behav-ioural ecology: an evolutionary approach, 4th ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 203–227.

Brown JL, 1987. Helping and communal breeding in birds: ecology and evolution. Princeton, New Jersey: Princeton University Press.

Brown JL, Pimm 1985. The origin of helping: the role of variability in reproductive potential. J Theor Biol 112:465–477.

Clarke MF, 1984. Co-operative breeding by the Australian bell miner, *Manorina melanophrys* Latham: a test of kin selection theory. Behav Ecol Sociobiol 14:137–146.

Clarke MF, 1989. The pattern of helping in the bell miner (*Manorina melanophrys*). Ethology 80:292–306.

Clutton-Brock TH, Parker GA, 1995. Punishment in animal societies. Nature 373:209–216.

Coeckelberghs SV, 1974. Territorial, spawning and parental behavior of *Lamprologus brichardi* Poll 1974 (Pisces, Cichlidae). Ann Soc R Zool Bel 105:73–86.

Creel SR, Waser PM, 1994. Inclusive fitness and reproductive success in dwarf mongooses. Behav Ecol 5:339–348.

Dierkes P, 1996. Genetischer Nachweis von Fortpflanzungsparisitismus durch Brutpflegehelfer bei *Lamprologus brichardi* einem Cichlidaen aus dem Tanganjika-See (MSc dissertation). Bielefield: University of Bielefeld.

Emlen ST, 1991. Evolution of cooperative breeding in birds and mam-mals. In: Behavioural ecology: an evolutionary approach (Krebs JR, Davies NB, eds). Oxford: Blackwell; 301–307.

Emlen ST, 1994. Benefits, constraints and the evolution of the family. Trends Ecol Evol 9:282–285.

Emlen ST, Wrege PH, 1988. The role of kinship in helping decisions among white-fronted bee-eaters. Behav Ecol Sociobiol 23:305–315.

Gaston AJ, 1978. The evolution of group territorial behavior and co-operative breeding. Am Nat 112:1091–1100.

Grantner A, Taborsky M, in press. The metabolic rates associated with resting and with the performance of agonistic, submissive and dig-ging behavior in the cichlid, *Neolamprologus pulcher* (Pisces: Cich-lidae). J Comp Physiol.

Hamilton WD, 1964. The genetical evolution of social behavior. I and II. J. Theor Biol 7:1–52.

Heinsohn RG, Cockburn A, 1994. Helping is costly to young birds in cooperatively breeding white-winged choughs. Proc R Soc Lond B 256:293–298.

Heinsohn RG, Cockburn A, Mulder RA, 1990. Avian cooperative breeding: old hypotheses and new directions. Trends Ecol Evol 5: 403–407.

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

Jamieson IG, 1989. Behavioral heterochrony and the evolution of birds' helping at the nest: an unselected consequences of commu-nal breeding? Am Nat 133: 394–406.

Komdeur J, 1992. Importance of habitat saturation and territory qual-ity for evolution of cooperative breeding in the Seychelles warbler. Nature 358:493–495.

Komdeur J, 1996. Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. Behav Ecol 7:326–333.

Ligon JD, Ligon SH, 1978. Communal breeding in green woodhoo-poes as a case for reciprocity. Nature 280:174.

Lawton MF, Guindon CF, 1981. Flock composition, breeding success, and learning in the brown jay. Condor 82:27–33.

Mech LD, 1970. The wolf: the ecology and behavior of an endangered species. New York: Natural History Press.

Mulder RA, Langmore NE, 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. Anim Behav 45:830–833.

Pruett-Jones SG, Lewis MJ, 1990. Habitat limitation and sex ratio pro-mote delayed dispersal in superb fairy wrens. Nature 348:541–542.

Reyer HU, 1980. Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis*). Behav Ecol Sociobiol 6:219–227.

Reyer HU, 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). Anim Behav 32:1163–1178.

Reyer HU, 1986. Breeder-helper interactions in the pied kingfisher reflect the costs and benefits of cooperative breeding. Behavior 96: 277–303.

Riedman MG, 1982. The evolution of alloparental care and adoption in mammals and birds. Q Rev Biol 57:405–435.

Rood JP, 1978. Dwarf mongoose helpers at the den. Z Tierpsychol 48: 277–287.

Rood JP, 1990. Group size, survival, reproduction and routes to breed-ing in dwarf mongooses. Anim Behav 39:566–572.

Rowley I, Russell E, 1990. Splendid fairy-wrens: demonstrating the importance of longevity. In: Cooperative breeding in birds: long terms studies of ecology and behavior (Stacey PB, Koenig WD, eds). Cambridge: Cambridge University Press; 1–30.

Solomon NG, French JA, 1997. Cooperative breeding in mammals. Cambridge: Cambridge University Press.

Stacey PB, Koenig WD, 1990. Cooperative breeding in birds: long terms studies of ecology and behavior. Cambridge: Cambridge Uni-versity Press.

Taborsky M, 1982. Brutpfegehelfer beim Cichliden *Lamprologus bri-chardi* Poll (1974): eine Kosten/Netzen-Analyse (PhD dissertation). Vienna: University of Vienna.

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 brood-care helpers: an experimental analysis. Behavior 95:45–75.

Taborsky M, 1994. Parasitism and alternative reproductive strategies in fish. Adv Study Behav 23:1–100.

Taborsky M, Grantner A, in press. Behavioural time-energy budgets of cooperatively breeding *Neolamprologus pulcher* (Pisces: Cichli-dae). Anim Behav.

Taborsky M, Limberger D, 1981. Helpers in fish. Behav Ecol Sociobiol 8:143–145.

Trivers RL, 1971. The evolution of reciprocal altruism. Q Rev Biol 46: 35–57.

Woolfenden GE, Fitzpatrick JW, 1978. The inheritance of territory in group-breeding birds. Bioscience 28:104–108.

Woolfenden GE, Fitzpatrick JW, 1984. The Florida scrub jay: demog-raphy of a cooperative-breeding bird. Princeton, New Jersey: Prince-ton University Press.

Zahavi A, 1976. Cooperative nesting in Eurasian birds. In: Proceedings of the 16th International Ornithological Congress, Canberra, Aus-tralia, 1975 (Frith HJ, Calaby JH, eds). Canberra: Australian Acad-emy Science; 685–693.