



Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish

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In social groups, subordinates may gain dominant breeding status either by inheriting the top position in their current group or by dispersing to join a new group. The pathway to breeder status is likely to vary between males and females as a result of sex differences in the costs of dispersal and inbreeding. We report results from a field study conducted to explore sex differences in the rates of territory joining and inheritance in a cooperatively breeding cichlid, *Neolamprologus pulcher*. We experimentally created 34 breeding vacancies and investigated the effects of breeder removal on the degree of cooperative behaviour and how changes in status influenced reproductive physiology. We found that 71% of male vacancies were filled by joiners (incoming fish, not previously members of the group) entering the territory. In contrast, only 15% of female vacancies were filled by joiners entering the group from elsewhere. Helpers increased their frequency of cooperative behaviour following the removal of a female breeder, but not following removal of a male breeder. Our results suggest that female breeder vacancies are typically filled by subordinate helpers who inherit from within the group and that male breeder vacancies are commonly filled by joining individuals (existing breeders or former helpers from other groups). Male social status and gonadal investment were positively correlated. This study represents one of the first experimental attempts to examine sexual differences in the pathway to breeding status in a cooperatively breeding species.

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In cooperatively breeding species, subordinate helpers can achieve the dominant breeding position by (1) inheriting the group/territory in which they had previously helped or (2) joining a new territory (Kokko & Ekman 2002). Helpers may fill a vacated breeding position or evict a current breeder when they inherit or when they join a new group. In some species, territory inheritance appears to be the more common method of becoming a breeder (Buston 2004), but in other species, individuals must move to join a new territory to mate (Doolan & MacDonald 1996). Variation in the pathway to breeding status is also likely to occur within a species, with one sex dispersing to achieve breeding status and the other inheriting a breeding position (Holekamp & Sherman 1989). Sex-specific differences in rates of territory inheritance and territory joining may be driven by sexual asymmetries in dispersal costs (e.g. differential costs associated with risk of predation or a reduction in feeding opportunities during dispersal) and/or dispersal benefits (such as inbreeding avoidance).

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These costs and benefits often lead to sex-biased patterns of dispersal (Pusey 1987).

In cooperative breeders, various patterns of sex-biased dispersal have been observed. In some species, females retain natal territories and males disperse (Holekamp & Sherman 1989), and in others, females disperse from the natal territories and males inherit (Pruett-Jones & Lewis 1990; Komdeur & Edelaar 2001; Cockburn et al. 2003). Similarly, Goldizen et al. (2002) showed that male Tasmanian native hens were more likely to inherit the breeding position in their natal group than females were. However, in other species, both sexes disperse to gain a breeding position (Doolan & MacDonald 1996; Clutton-Brock et al. 2002).

To examine sex differences in the rates of territory inheritance versus territory joining, we created breeding vacancies by removing breeders from social groups of the cooperatively breeding cichlid, *Neolamprologus pulcher*. Breeder turnover in this species is common in the field (Taborsky 2001; Stiver et al. 2004), so such experimental removals are likely to imitate natural events. Two factors of *N. pulcher* life history suggest that males experience increased benefits and decreased costs associated with

dispersal compared to females and are therefore more likely to disperse to join new territories than are females. First, helpers are more related to the breeding female than the breeding male (Stiver et al. 2005), probably because of the shorter breeding tenure of males (Stiver et al. 2004); therefore, the risk of an inheriting individual mating with their parent (and suffering inbreeding costs) is greater for males than females. Second, male *N. pulcher* grow larger than females (Balshine et al. 2001); this larger body size may lower the cost of dispersing by reducing predation risk (Paine 1976). Predation pressure constrains dispersal in *N. pulcher* (Heg et al. 2004). In fact, dispersal may indeed be male biased (Stiver et al. 2004). Based on a small group of resampled individuals (14 individuals recaptured after a year), two distant dispersal events by male helpers were confirmed. These males had become breeders in new territories. Moreover, comparison of within-sex pairwise relatedness values between subpopulations also suggests male-biased dispersal (Stiver et al. 2004).

In addition to creating a new breeding opportunity for one individual, breeder removals may signal to helpers that there has been a change in their relatedness to the breeders as well as to future young emerging from that territory. Therefore, we predicted that, following a replacement event, the helping behaviour of individuals remaining in the group would be altered (Hamilton 1964; Kokko et al. 2002). Our breeder removal experiment offered the opportunity to test this idea in *N. pulcher* by examining the direction of change in helping behaviour following breeder removal and replacement events.

Finally, by removing breeders, we created opportunities for individuals to increase their social status. In other species, a change in social status has been shown to result in rapid gonadal growth (Warner & Swearer 1991; Munday et al. 1998; Hofmann et al. 1999). Hence, the aims of our study were to investigate the following three questions. (1) Are there sex differences in the likelihood of joining or inheriting a territory? (2) Are there changes in helping effort following a breeder removal and replacement event, and if so, what are the nature of these changes? (3) What physiological changes occur in individuals who rise in the social dominance hierarchy?

METHODS

Study Species

Neolamprologus pulcher is a cooperatively breeding cichlid fish endemic to Lake Tanganyika, Africa. Social groups are made up of one breeder of each sex and 1–15 'helpers' of both sexes (Balshine et al. 2001). These helpers are socially subordinate individuals in the group who assist in territory maintenance (i.e. removing substrate from the brood chamber and shelter system), territory defence (from predators and space competitors) and brood care (i.e. fanning and cleaning eggs; Taborsky & Limberger 1981; Taborsky 1984). Some helpers are sexually mature individuals, and it has been suggested that male helpers can share paternity with the dominant breeding male (Dierkes et al. 1999; Dierkes 2004; but see Fitzpatrick

et al. 2005). Additionally, breeding males may be harem, holding multiple breeding territories, with a breeding female in each (Limberger 1983). Each group occupies a territory at depths of 3–45 m along the lakeshore (Taborsky & Limberger 1981). Territories (median size = 3150 cm²) in our study area consisted of rocks on sandy substrate. Territories are clustered into distinct subpopulations of two to over 100 territories (Balshine et al. 2001; K. Stiver, S. Balshine & M. Taborsky, personal observation).

Protocols

Field work was conducted between March and April of 2004 on the Zambian shores of Lake Tanganyika in Kasakalawe Bay. Groups of *N. pulcher* were located and monitored at 8.5–11.5 m depth using SCUBA. All data and behavioural observations were recorded on PVC plates. The study area and general field methods are described elsewhere (Balshine-Earn et al. 1998; Balshine et al. 2001; Werner et al. 2003; Stiver et al. 2004).

Twenty-one breeders (8 males, 13 females) were removed from their groups. The eight male removals created a total of 21 male breeding vacancies, because seven of these males were polygynous males that held the dominant breeding position in two or more groups ($\bar{X} \pm \text{SE}$ harem size = 2.86 ± 0.26). Therefore, we created 34 breeding vacancies (13 female, 21 male). Before the removal, both breeders and one to two large focal helpers were captured from each group using acrylic tubes and handnets. Each individual's standard length was measured, its sex determined (by examination of the genital papilla), and then it was marked by a subcutaneous injection of non-toxic acrylic paint in one of 16 unique body locations. The capture and marking techniques did not appear to harm the fish, and they were swimming normally around their territory within 2–5 min following initial capture (see Balshine-Earn et al. 1998; Balshine et al. 2001).

Each breeder and the two largest helpers in each group were observed (focal observations) for 10 min; we recorded feeding, defence (against conspecifics and heterospecifics), number and duration of brood chamber visits, territory maintenance (digging and carrying) and intragroup interactions (aggression, submission, social behaviours and courtship). Slow deliberate nudges between individuals within a group were classified as 'social behaviour'. We use the term 'work effort' to refer to the cumulative acts of helping (i.e. the total number of brood chamber visits in addition to total number of territory defence and territory maintenance acts). The behavioural repertoire of this species is described in detail elsewhere (Kalas 1975; Grantner & Taborsky 1998; Buchner et al. 2004).

Following these initial behavioural observations ('before' observations), a targeted breeder was captured and removed from each group. All remaining individuals initially observed were watched both 24 and 96 h following the breeder removal. New individuals observed to have joined the groups were recorded and observed for 10 min (once or twice, depending on whether they had

joined within 24 or 96 h after removal), and any missing group members were noted. Following the 96-h observation periods, entire groups were collected using acrylic tubes, nets and 3–7 ml of quinaldine (2-methylquinoline; $C_6H_4N:C(CH_3)CH:CH$, a common fish anaesthetic). At the surface, we measured standard length (± 0.01 cm) and body mass (± 0.001 g). The fish were killed using an overdose of ethyl 4-aminobenzoate (Sigma-Aldrich, St Louis, Missouri, U.S.A.) and cervical severance, and sexed by examination of gonads.

Physiological Analyses

Gonads were removed from each sacrificed individual and weighed (± 0.001 g). Gonadal investment was measured using the gonadosomatic index, $GSI = (\text{gonad mass/body mass}) \times 100$, to control for body mass.

Statistical Analyses

Before analyses, all variables were tested for normality and equality of variances; when data could not be transformed to fit the criteria of a parametric test, the equivalent nonparametric test was used. Statistical analyses were performed using StatView 4.0 (1992–1998, SAS Institute Inc., Cary, North Carolina, U.S.A.) for Macintosh, although when sample sizes were small, some nonparametric tests were calculated by hand (Mundry & Fischer 1998). All P values reported are two tailed and corrected for ties. Apart from feeding, the frequency of the behaviours recorded (within classes of individuals) did not differ between day 1 (24 h) and 4 (96 h) postremoval; therefore, the observations from both days (apart from feeding) were averaged to create a single mean value for each specific behaviour (the ‘after’ removal observation).

Notes on Terminology

A helper was defined as a ‘candidate inheritor’ when its standard body length fell within the 95% confidence interval of breeders of its sex. Candidate helpers were present in seven of 21 male removal groups and in six of 13 female removal groups. Breeder replacement was defined to occur when an individual not previously affiliated with the group (of the removed sex and breeder size) joined the group as a ‘territory joiner’, or when a candidate helper within the group became the dominant individual of that sex with no outsider joining; this individual was called a ‘territory inheritor’.

Ethical Note

All research described conformed to the protocols approved by the Animal Research Ethics Board of McMaster University and Canadian Council for Animal Care guidelines and was conducted with the permission and cooperation of the Zambian Department of Fisheries. Care was taken to minimize stress to the fish used in this study.

RESULTS

Breeder Replacement

Breeder replacement occurred in 76% (26 of 34) of all breeding vacancies created (Fig. 1). New males joined male removal groups more frequently (71% of cases) than new females joined female removal groups (15% of cases, log-linear G test: $G_1^2 = 10.84$, $P = 0.03$; Fig. 2).

When we examined only groups known to contain a candidate helper, still more joining occurred in male breeder removal groups than the female breeder removal

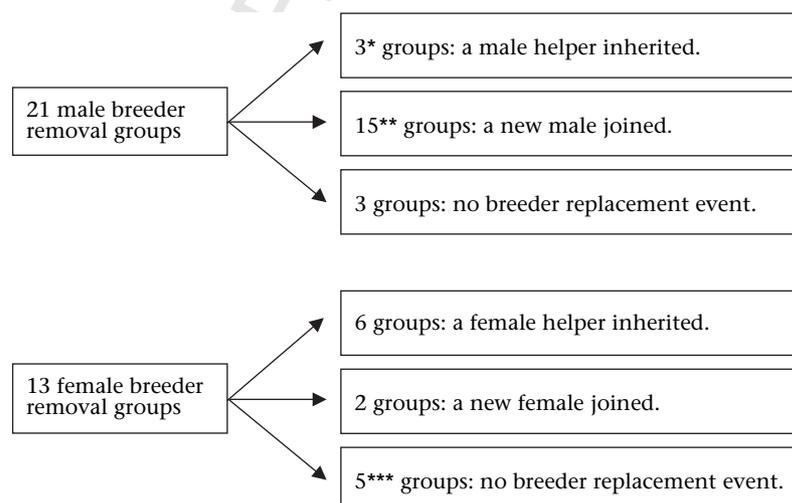


Figure 1. Outcomes of breeder removal trials (number of joining and inheritance events). *One of the male inheritors also took over a neighbouring vacancy. **Two joining males were former helpers from other groups (one took over two vacancies, and one was both an inheriting male and a joiner who also took over a neighbouring vacancy; see above). The remaining vacancies were filled by nine established breeder males (one took over three vacancies, one took over two, and the remaining seven males took over one vacancy each). ***In three of these groups, all but one helper disappeared by day 1 postremoval; in these three groups and one other group in which helpers did not disappear, the remaining male breeder decreased the time spent on the territory by 99%.

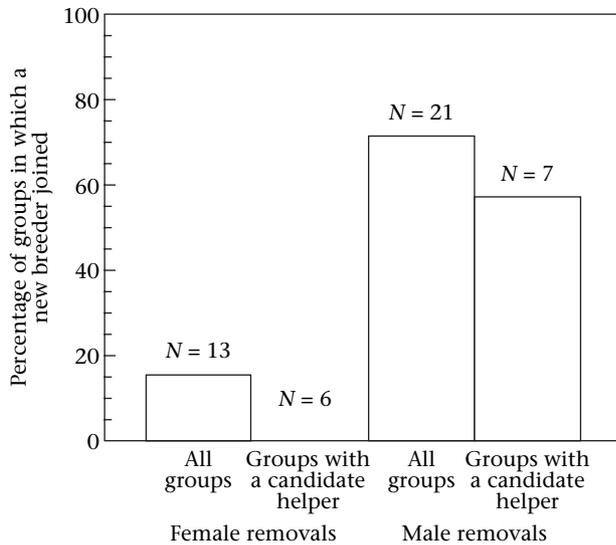


Figure 2. Comparison of joining rates following male breeder and female breeder removals. Rates are presented as the percentage of vacancies filled by a joining individual in all groups and only in those groups containing a candidate helper capable of territory inheritance.

groups G test: $G_1^2 = 6.09$, $P = 0.01$; Fig. 2). In these groups, helpers inherited in 100% of female removal groups, but helpers inherited in only 43% of male removal territories. These results indicate that the difference in inheritance and joining rates were not a result of differences in the ratio of candidate helpers in male and female removal groups. However, although *N. pulcher* breeding males can hold harems, simultaneously breeding in more than one group, breeding females do not do this (Limberger 1983). Therefore, although female *N. pulcher* breeders from neighbouring groups were not potential joiners who could fill a vacated breeding position, established male breeders from nearby territories could join and take over one of the vacancies created while still holding on to their original territories. When these established breeding males were removed from the analyses, no difference was found in joining rates between male ($N = 10$) and female removal groups ($N = 13$; G test: $G_1^2 = 1.78$, $P = 0.18$). This result suggests that the observed difference in joining and inheritance rates of males and females may result from the different reproductive strategies available to males and females.

Evidence suggests that dispersal and joining rates are influenced by group size (Herrera & Macdonald 1993; Stephens et al. 2005; but see Field et al. 1999). We did not manipulate group size, but groups from which we removed breeders ranged from 4 to 14 individuals (mean group size = 7.5 individuals). The likelihood of a joining event was not influenced by group size (mean size male removal groups = 7.7, female removal groups = 7.2; Mann-Whitney U test: $U = 126$, $N_1 = N_2 = 17$, $P = 0.52$). This was also true when we examined male and female removal groups separately (male breeder removals: $U = 38$, $N_1 = 15$, $N_2 = 6$, $P = 0.58$; female breeder removals: $U = 10.5$, $N_1 = 2$, $N_2 = 11$, $P = 0.92$).

Behavioural Changes

Helpers and remaining breeders

Feeding decreased following the male removals, but this difference was only significant at 24 h postremoval (Friedman test: $\chi_2^2 = 14.66$, $N = 55$, $P = 0.001$). This difference was not observed following female removals ($\chi_2^2 = 0.23$, $N = 28$, $P = 0.89$).

Helpers

In all groups that experienced an inheritance event, helpers tended to increase work effort (Wilcoxon signed-ranks test: $T = -15.5$, $N = 10$, $P = 0.06$), no differences in work effort were detected following joining events ($Z = -0.24$, $N = 24$, $P = 0.81$).

Helpers that maintained their helper status increased helping (work effort) following female breeder removals ($T = -34.0$, $N = 14$, $P = 0.02$; Fig. 3a), but this was not the case in groups experiencing male breeder removal ($Z = -0.41$, $N = 29$, $P = 0.68$; Fig. 3b). All helpers remaining in helper status (in both male and female removal groups) increased their submissive behaviour following

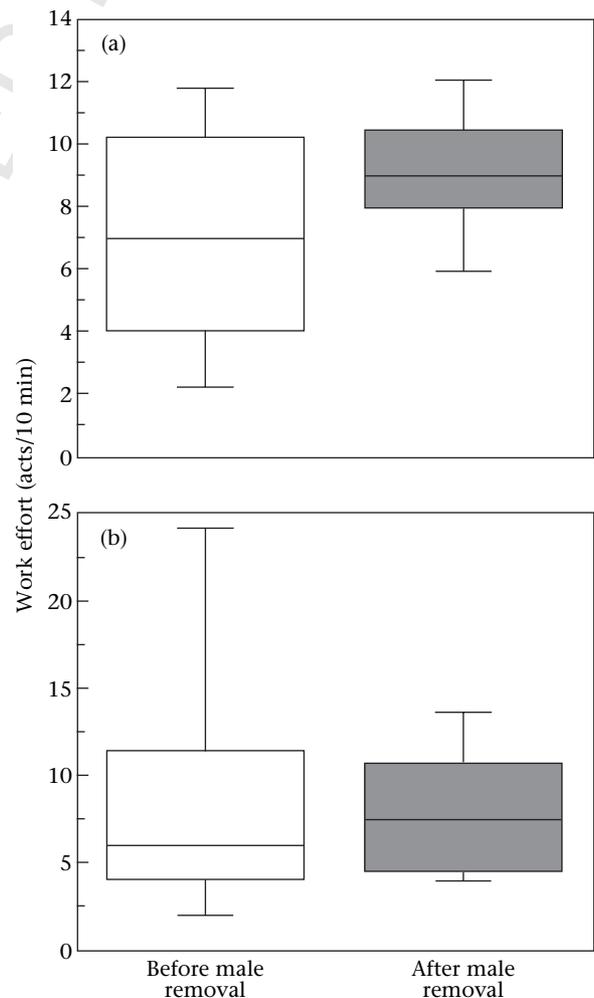


Figure 3. Rates of work effort (brood chamber visits + territory defence acts + territory maintenance acts), by helpers, before and after (a) female breeder removals and (b) male breeder removals.

breeder removals ($Z = -2.07$, $N = 43$, $P = 0.04$). In male removal groups, helpers that maintained their helper status were also more aggressive after removals ($Z = -2.09$, $N = 31$, $P = 0.04$).

New versus removed breeders

We found no behavioural differences between the replacement breeders and the original breeders, supporting the hypothesis that these individuals did take over the position of the removed breeders (Table 1).

Note on relatedness

Based on genetic data from *N. pulcher* groups collected for two previous studies on the same study population (Stiver et al. 2004, 2005), we calculated that helpers are typically more related to candidate helpers in their group than they are to the breeders (Wilcoxon signed-ranks test: $Z = -2.565$, $N = 87$, $P = 0.010$). Thus, helpers whose group's breeding vacancy was filled by an inheritor were likely to have experienced an increase in their relatedness to that breeder.

Physiological Differences

Males

No body size (length or mass) differences were detected among original removed breeders ($N = 8$), previously existing breeding males who increased their harem size by joining the removal groups ($N = 4$), former helpers that became breeders ($N = 4$) and male helpers that failed to inherit a breeding vacancy ($N = 3$; Kruskal–Wallis ANOVA: body length SL: $H_3 = 6.8$, $P = 0.08$; body mass: $H_3 = 6.64$, $P = 0.08$). Both absolute and relative (GSI) testes mass (in grams) differed significantly between the four classes of males (absolute testes mass: $H_3 = 10.26$, $P = 0.02$, Fig. 4a; GSI: $H_3 = 9.67$, $P = 0.02$, Fig. 4b).

Females

There were no somatic (body length or mass) or gonadal investment differences between the removed female breeders ($N = 13$) and former female helpers that became breeders (territory inheritors, $N = 6$; Mann–Whitney U test: body length SL: $U = 36.0$, $P = 0.79$; body mass:

Table 1. The median frequency of various behaviours (per 10 min of focal observation)

Behaviour	Original breeder	Replacement breeder	Test statistic	P
Feeding	205	Day 1: 99 Day 4: 155	$\chi^2_2 = 2.63$	0.27
Work effort	5.5	5.5	$Z = -0.18$	0.86
Aggressive acts	0.5	0.75	$Z = -0.79$	0.43
Submissive acts	0.0	0.0	$Z = -1.41$	0.16
Social acts	0.0	0.5	$Z = -0.07$	0.94

Wilcoxon signed-ranks tests were used (except for feeding, where a Friedman test was used). There were $N = 16$ replacement breeders (10 males, 6 females) whose behaviour on both days 1 and 4 post-removal could be compared to that of the original breeder.

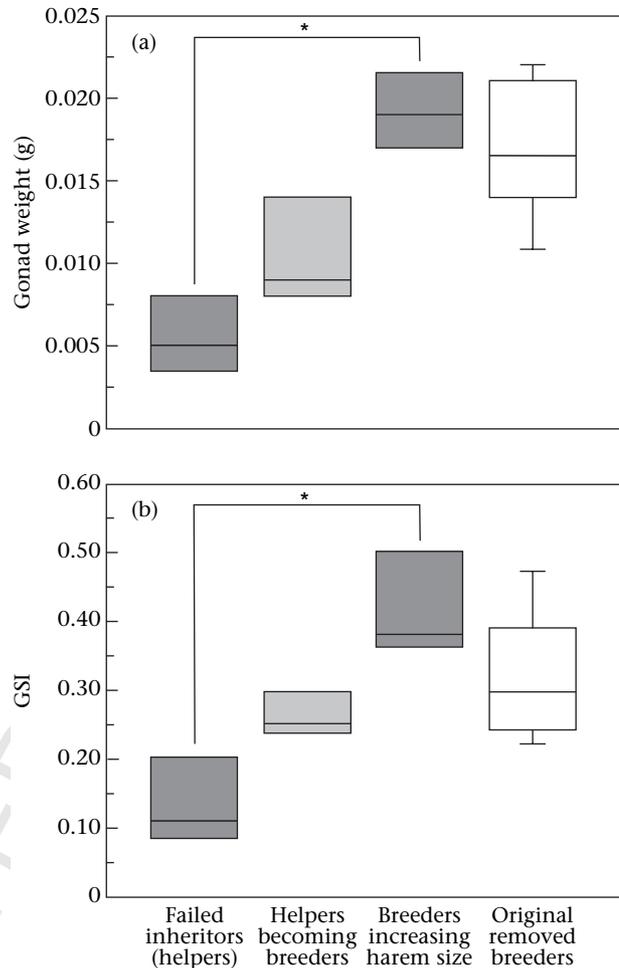


Figure 4. Differences in (a) absolute gonad masses and (b) relative gonad masses (GSI) among original removed breeding males, established breeders who enlarged their harem, helper males who became breeding males and candidate males that failed to inherit ($*P < 0.05$).

$U = 27.5$, $P = 0.31$; absolute gonad mass: $U = 27.0$, $P = 0.29$; relative gonad mass (GSI): $U = 29.5$, $P = 0.40$). Although the sex of the two joining females was confirmed, we were unable to take further physiological measures on those individuals because they escaped during transport and were therefore excluded from analyses (we had no failed female inheritors, so these individuals were not available for comparison).

DISCUSSION

Are There Sex Differences in Joining and Inheritance Rates?

Our results suggest a sex difference in the strategy used to become a breeder; it appears that typically, males join, and females inherit to breed. The difference is primarily because of a difference between the reproductive opportunities available to males and females; established male breeders often compete and win breeding vacancies, but established female breeders do not. Male helpers are likely

to have a hard time competing with established male breeders. Therefore, while dispersal may be potentially costly for both sexes (although perhaps slightly less so for males, because of their larger body size), the potential benefits of dispersal may be far greater for males, leading to a sex difference in how mature individuals typically attain a breeding position. Although we did observe the occasional true male dispersal event, more generally, males who took over breeding territories already held territories of their own and did not disperse in the traditional sense. Rather, they expanded their home range to encompass the territories of multiple breeding females. The results suggest that dispersal and expansion events by males are the primary force behind gene flow in this species.

Other researchers have experimentally created breeding vacancies with mixed results. For example, in eusocial hover wasps, *Liostenogaster falvolineata*, helpers rarely took over vacancies (Field et al. 1998). In two previous field studies, researchers removed *Neolamprologus* breeders, but did not examine how behaviour of the group or physiology of the new breeders was altered following the breeder turnover. In the first study, conducted on *N. brichardi*, a sister or subspecies of *N. pulcher* (Grantner & Taborsky 1998), researchers found no instances of territory inheritance following breeder removals and 100% of the groups experienced joining (Taborsky & Limberger 1981; Taborsky 1984; the number of male and female breeders removed was not reported). In a second study conducted on *N. pulcher*, helpers from within the group inherited the territory in approximately 40% of the groups and joining occurred in 60% of the groups (Balshine-Earn et al. 1998). Our findings mirror these results, but we observed a sex difference in joining rates not previously reported. The difference in joining and inheritance rates between *N. brichardi* and *N. pulcher* helpers is probably a result of differences in life history stages. *Neolamprologus brichardi* helpers (but not *N. pulcher* helpers) typically depart at sexual maturity to join nonreproductive aggregations until they are able to join a territory and gain a mate (Taborsky & Limberger 1981; Taborsky 1984).

Are There Behavioural Changes Following a Breeder Removal and Replacement?

Helpers in groups where the breeding vacancy was filled by an inheritor probably experienced an increase in their relatedness (because helpers were more related to candidate inheritors than they were to breeders). Helpers experiencing a joining event were likely to be less related to the new breeder than to the removed one. If helpers gain inclusive fitness by assisting relatives (Hamilton 1964; Stiver et al. 2005), more help is expected following an inheritance event, and less help is expected following a joining event. Alternatively, if helpers help primarily as a means of paying rent to breeders, (pay-to-stay theory: Gaston 1978), unrelated individuals might actually be expected to 'pay' more (Balshine-Earn et al. 1998; Kokko et al. 2002; Bergmüller & Taborsky 2004; Bergmüller et al. 2005; Hamilton & Taborsky 2005; Stiver et al.

2005). Under these circumstances, helpers might be expected to help more following a joining event and help less following an inheritance event. In our study, helpers tended to increase help in all groups that experienced an inheritance event; however, no difference was detected in helping effort following joining events.

The majority of inheritance occurred in female removal groups, and most of the joining occurred in male removal groups. Helpers in female (but not male) removal groups helped significantly more following removal. Most female removal groups gained a new breeder through inheritance, so helpers in female breeder removal groups were more likely to be related to the replacement female breeder than to the removed female breeder. Increased helping behaviour following inheritance events suggests that helpers adjust investment in accordance with kin selection theory (Hamilton 1964).

A decrease in helping effort was not detected in the male removal groups that mainly experienced joining events. Why was this decrease not found if kin selection is operating in this species? In *N. pulcher*, male breeder turnover occurs twice as often as female breeder turnover (Stiver et al. 2004), leading to higher relatedness values between helpers and breeding females (Stiver et al. 2005). Helpers are typically less related to the breeding male than to the breeding females; therefore, the loss of a female breeder may provide helpers with more relevant information with regard to a change in relatedness to potential future young. This hypothesis may help to explain why we observed an adjustment in the amount of help performed following breeder turnover (and a cue of change in relatedness of the helper to the breeder) only in helpers in female removal groups.

There are two other possible reasons why helpers increased helping behaviour in these groups. First, when the breeding female was removed, typically no new female joined, resulting in a decrease in overall group size. This decrease may have required each remaining individual to perform more work, causing the observed increase in helping behaviour. This explanation is less likely than the one above, because an increased need for work should have manifested in increased work effort by all group members, and we observed no such increase in work effort by the breeders. Second, inheritance means that remaining helpers have moved up in the breeding queue, and as the expectation of future benefits increase, helpers might be more willing to help (to ensure a workforce once they inherit: Shreeves et al. 2003). In contrast, Cant & Field (2001) predicted that most dominant helpers (or next-in-line helpers) hold back, 'saving' energy for eventual take-overs. We did not test between these two alternatives; further work consisting of dominant helper removals are needed to address this issue.

Breeder removal had an overall destabilizing effect on group dynamics and altered group behaviour. All helpers performed more submissive behaviour and, in the groups where a male was removed, helpers were also more aggressive towards members of their group. Loss of the breeding female may be particularly destabilizing to a *N. pulcher* group. There was an apparent collapse of three female removal groups (where the majority of the helpers

disappeared) that occurred within 24 h of removal. Breeding males in these defunct groups greatly decreased the time they spent in these territories; essentially, two breeders had left these groups. Male breeders often hold more than one territory and hence have a greater number of reproductive options available to them. It may be unprofitable for a male to continue patrolling and defending a territory that no longer contains a potential mate. The abandonment by the male may have triggered the subsequent dispersal of the helpers. Breeding females, in contrast, were not observed to decrease time spent on a territory following male removals.

Were There Physiological Changes in Individuals Who Increased in Status?

Gonad size (both absolute and relative) of removed female breeders was no different than that of the inheriting females. Removed male breeders and established male breeders who increased their harem size appeared to have larger testes and GSIs than did helpers who failed to inherit a breeding position. Males who moved from helper to breeder status had intermediate-sized testes. These results suggest that inheriting males were in the process of increasing their gonadal mass. These results imply a rather dramatic temporal increase in investment, similar to gonadal growth and development that has been documented after 1 week in another cichlid fish (*Haplochromis burtoni*: Hofmann et al. 1999) and after 1 month in blueheaded wrasse (*Thalassoma bifasciatum*: Warner & Swearer 1991). Alternatively, the differences in testes size may, reflect a predisposition of some males to be more successful in filling a vacated breeding position, rather than a change in response to an increase in status. The mechanisms underlying gonadal investment in relation to changes in social status for both sexes is the subject of current investigation in our laboratory.

Our results show that changes in the dominance hierarchy (specifically, the loss of a breeder) can affect the behaviour and physiology of individuals living in a social group. In support of kin selection, helpers appeared to help more when they experienced an inheritance event (a potential cue of an increase in relatedness to the breeding female). Males that increased in status had larger gonads than did nonascending males. Breeding vacancies appear to provide sex-specific expansion opportunities and highlight the life history trade-offs underlying sex differences in territory inheritance and joining in a cichlid fish.

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