Behavioral Ecology
doi:10.1093/beheco/arr218
Advance Access publication 20 January 2012

Original Article

Mating systems in cooperative breeders: the roles of resource dispersion and conflict mitigation

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Within animal societies, the ecological and social underpinnings of mating system variation can be related to resource dispersion, sexual conflict between breeders, and the effects of non-breeders. Here, we conducted a broad-scale investigation into the evolution of mating systems in the cooperatively breeding cichlid, *Neolamprologus pulcher*, a species that exhibits both monogamy and polygyny within populations. Using long-term field data, we showed that polygynous groups were more spatially clustered and held by larger competitively superior males than were monogamous groups, supporting the role of resource dispersion. To explore the role of sexual conflict, we forced polygynous males to become experimentally monogamous (EM) in the field. EM males spent more time on their remaining territory than naturally polygynous males but otherwise did not change behaviorally or physiologically. Females mated to EM males performed more submissive acts, and in a forced choice experiment, females did not preferentially associate with the larger of two unmated males. Females may therefore incur an unexpected cost from mating monogamously with a large and competitively superior male, a cost that mitigates sexual conflict over the mating system. Helpers were more closely related in monogamous groups but did not behave differently under monogamy or polygyny. Helpers therefore seem neither to be affected by nor affect the mating system of breeders. Our results demonstrate the roles of resource availability and conflict mitigation in determining the mating system, and highlight the importance of experimental manipulation for revealing hidden costs of hypothetical mating patterns. *Key words:* cooperative breeding, mating system, monogamy, polygyny, resource dispersion, sexual conflict. *[Behav Ecol 23:521–530 (2012)]*

INTRODUCTION

Understanding the factors shaping the evolution of mating systems is an enduring challenge in evolutionary and behavioral ecology (Orians 1969; Emlen and Oring 1977; Reynolds 1996; Shuster and Wade 2003; Owens 2006). The attraction of researchers to breeding behavior stems in part from the enormous diversity of mating systems exhibited both within and between species (Davies 1985; Reynolds 1996; Allainé 2000; Shuster and Wade 2003; Hernamen and Munday 2007). Over the last 40 years, a wealth of theoretical explanations have emerged in an attempt to explain this extraordinary variation (Orians 1969; Emlen and Oring 1977; Kleiman 1977; Wittenberger and Tilson 1980; Wickler and Seibt 1981; Mock and Fujioka 1990; Shuster and Wade 2003). The most influential theory for mating system evolution is the Environmental Potential for Polygyny (EPP) model, which links the mating system to the distribution of limiting resources and hence females which map onto those resources (Emlen and Oring 1977). When resources are clustered in space, females will also tend toward a clustered distribution, allowing males to monopolize multiple females and achieve their preferred polygynous status. Conversely, when resources and females are widely dispersed, males are unable to monopolize multiple females and so must settle with mating monogamously (Emlen and Oring 1977). This model therefore predicts a close association between monogamy, dispersed females, and competitively inferior males, and between polygyny, clustered females, and competitively superior males (Kleiman 1977; Rutberg 1983; Vehrencamp and Bradbury 1984; Clutton-Brock 1989; Travis et al. 1995).

Mating systems can also be affected by sexual conflict between males and females (Davies 1982; Arnqvist and Rowe 2005; Chapman 2006). In species where males provide parental care, males can face a trade-off between mating and

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Received 6 July 2011; revised 29 November 2011; accepted 3 December 2011.

parental effort (Magrath and Komdeur 2003; Kokko and Jennions 2008). In general, males can maximize their reproductive success by monopolizing multiple females, but such polygamy may not be in the best interest of females because each receives less parental effort from the male compared to if he was monogamous (Slagsvold and Lifjeld 1994; Smith and Sandell 1998; Pribil 2000; Kokita and Nakazono 2001). Various factors can influence the intensity of such sexual conflict. For example, a males' phenotype could determine his capacity to gain additional mating and compete with members of the same sex over breeding opportunities. Several traits, including body size and age, are often positively related to male competitive ability and quality. Thus, larger, older, and more competitive males are expected to invest more in becoming polygynous and hence provide less care as a result (Mitchell et al. 2007). Conversely, smaller, younger, and less competitive males are expected to invest less in competing over females and instead allocate resources to providing more parental care (Fromhage et al. 2005; Kokko and Jennions 2008). Therefore, females often face a trade-off between male quality versus male care that influences their mating choices. When part of a polygynous group, females may be compensated for reduced male care by high male quality, whereas when part of a monogamous group, females are compensated for low male quality by increased male care (Webster 1991; Kempenaers 1994; Slagsvold and Lifjeld 1994; Desjardins, Fitzpatrick, et al. 2008).

Sexual conflict could also be mitigated by other factors besides male quality. In social species, the presence of auxiliary group members that provide alloparental care, as seen in cooperatively breeding species, could compensate females for reductions in male parental care (Mulder et al. 1994; Green et al. 1995; Webster et al. 2004). The level of care provided by helpers could furthermore be related to the degree of within-group relatedness, which itself could be influenced by the type of mating system expressed. When breeders are strictly monogamous, any nonbreeding offspring are as much related to their future siblings as they are to their own offspring, thus monogamy could select for higher degrees of cooperation than polygyny given suitable ecological conditions (Hughes et al. 2008; Boomsma 2009; Cornwallis et al. 2010). This in turn suggests that the mating system and associated degrees of relatedness may modulate the amount of compensatory help provided by helpers. Finally, understanding the proximate mechanisms controlling behavioral trade-offs could provide a more complete picture of sexual conflict. Androgen hormones, such as testosterone (T) and 11-ketotestosterone (11KT), have been implicated in the proximate control of reproductive, aggressive, and parental behavior in animals (Wingfield et al. 1990; Hirschenhauser and Oliveira 2006; Taves et al. 2009) and thus could play a key role in governing the intensity of sexual conflict and the type of mating system being expressed.

Here, we used the co-occurrence of monogamy and polygyny in a single population of the cooperatively breeding fish, *Neolamprologus pulcher*, to investigate the environmental, social, and genetic factors influencing mating systems. *Neolamprologus pulcher* is a cichlid endemic to Lake Tanganyika in Africa that forms social groups, which defend a discrete rocky territory (Taborsky and Limberger 1981). A social group of *N. pulcher* is made up of a dominant breeding pair and 0–20 smaller subordinates called helpers (Taborsky 1984, 1985; Wong and Balshine 2011). The breeding male is the largest group member, the breeding female usually the second largest, while subordinate helpers are smaller and organized into a size-based dominance hierarchy (Balshine-Earn et al. 1998; Heg, Bender, et al. 2004). Subordinate helpers assist breeders in territory defense, maintenance, and broodcare (Taborsky and Limberger 1981; Wong and Balshine 2011). While some researchers have treated *N. pulcher* as a monogamous species (Hirschenhauser et al. 2008), the existence of large males holding haremic positions in multiple groups has been known since the first investigations of *N. pulcher*'s behavior in the field (Limberger 1983), and polygyny confirmed in further investigations of the mating behavior of this species (Desjardins, Fitzpatrick, et al. 2008). Specifically, while the breeder female is socially pair-bonded to just one breeder male, breeder males can defend one or multiple territories each with its own breeder female and helpers (Limberger 1983; Desjardins, Fitzpatrick, et al. 2008). Thus, mating strategies vary between monogamy, in which males defend only one breeder female territory, to polygyny, in which males defend several female territories (Desjardins, Fitzpatrick, et al. 2008). Interestingly, males holding multiple females are larger, have higher concentrations of 11KT, higher gonadosomatic indices, and lower parasite loads than monogamous males, indicating that polygynous males are of higher quality than monogamous males (Desjardins, Fitzpatrick, et al. 2008). However, polygynous males provide less care than monogamous males, thus females face an apparent trade-off between male quality and care which is directly related to the mating system (Desjardins, Fitzpatrick, et al. 2008). This variability in mating systems combined with cooperative breeding makes *N. pulcher* an excellent model species for addressing the relationship between ecology, sexual conflicts, and mating system evolution.

We begin by expanding on the study by Desjardins, Fitzpatrick, et al. (2008) by comparing the ecological, behavioral, and genetic correlates of the mating system that spans 3 years of research on one natural population in Lake Tanganyika. Using these data, we first assessed whether the EPP underlies the variable mating system. If so, males should be polygynous when females are clustered in space and monogamous when females are widely dispersed. Second, we investigated whether associating with kin promotes female clumping and hence polygyny, by ameliorating any costs of polygyny for females (Emlen 1995; Pen and Kerth 2005). If kinship promotes clumping then females paired with polygynous males will be both more clumped in space and more related to their nearest neighbors than females paired with monogamous males. Third, we investigated the association between mating system, within-group relatedness, and helping effort to test the hypothesis that monogamy leads to increased relatedness, which in turn promotes cooperative behavior. Based on this hypothesis, we predicted that monogamous groups would be characterized by higher within-group relatedness and higher work effort by helpers than polygynous groups. We then performed a field manipulation in which large polygynous males were forced to accept a monogamous mating system. In so doing, we created an opportunity to investigate behavioral changes that may indicate the occurrence of sexual conflicts, and identify the proximate physiological mechanisms that may be implicated in the control of reproductive or parental care behavioral changes. We further investigated the nature of sexual conflicts by performing a mate choice experiment to elucidate whether males and females exhibit active preferences for larger or smaller mates. All in all, we incorporate behavioral, morphological, physiological, and genetic data to investigate the combined effects of resource dispersion, sexual conflict, and sociality on mating system evolution in a social species.

MATERIALS AND METHODS

Study site and general methods

The study site was situated in Kasakalawe Bay on the Zambian shores of Lake Tanganyika, 100 m east of Kasakalawe village (8°46′S; 31°46′E). Between March–April 2004, February–April 2005, and October–December 2008, data on group composition and social mating system were collected using self contained underwater breathing apparatus (SCUBA). Fish were collected with polyvinyl chloride tubes, hand and barrier nets and placed individually into temporarily sealable mesh bags where body size was measured to the nearest 0.1 cm standard length (SL) using flexible rulers. The distance to a groups' nearest conspecific group was measured using a measuring tape. Mating system was initially assessed by conducting two or three 5 min observations on each group to determine the number of helpers in each group and the number of female territories held by each breeder male (see Desjardins, Fitzpatrick, et al. 2008). Groups were classified as being monogamous (breeder male controlled one territory) or polygynous (breeder male controlled multiple territories) based on the number of territories held by the breeder male. Fin clips of group members were collected from either the dorsal or anal fin and preserved in 95% ethanol for later genetic analysis (for details on the genetic protocol, see Stiver et al. 2005, 2007, 2009).

Does the EPP explain the variable mating system?

Using field data from 2004 to 2005, we quantified the spatial distribution of monogamous ($N = 38$) and polygynous ($N = 45$) groups by measuring nearest-neighbor distances for both monogamous and polygynous territories (using a larger sample size than what has been reported previously in Desjardins, Fitzpatrick, et al. 2008). Nearest-neighbor distances were defined as the shortest distance between each focal monogamous or polygynous group and their nearest neighboring social *N. pulcher* group. Fin clips were taken from individuals in these groups and used to calculate pairwise relatedness between breeding females based on microsatellite loci (for protocol, see Stiver et al. 2005, 2007, 2009).

Does mating behavior influence levels of cooperation by helpers?

Based on genetic data from fin clips collected in 2004 and 2005, the average pairwise relatedness between group members was quantified for both monogamous ($N = 70$) and polygynous ($N = 65$) groups. We investigated the correlation between overall work effort performed by helpers (the summed frequency over a 10 min period of the number of territory maintenance events, defense behaviors, and brood chamber visits) and the degree of relatedness between helpers and between helpers and breeders within the group, for a subset of monogamous ($N = 20$) and polygynous groups ($N = 34$). In all these analyses, helper size and sex were controlled for, as these factors have previously been shown to correlate with work effort (Stiver et al. 2005).

Does sexual conflict between breeders influence the mating system?

A field manipulation experiment was conducted between 26th October 2008 and 11th December 2008 in Kasakalawe Bay. A total of 21 "naturally polygynous" (NP) male territories were located using SCUBA at a depth of 8–12 m. The NP territories were randomly assigned to either a control ($N = 10$ groups) or removal ($N = 11$ groups) treatment. For each NP male, one of his breeding females and all her helpers were randomly assigned to be the "focal" group, and in this focal group, the NP breeder male, breeder female, a large helper (>4 cm), and a small helper (<4 cm) were chosen as focal individuals for observations. These focal individuals were collected, measured, sexed (based on the shape of the genital papilla), and marked underwater using injections of colored fluorescent elastomer (Northwest Marine Technology Inc., Shaw Island, WA) at different positions along the dorsal musculature and released back into their rocky territory.

The following day (Day 0), each focal individual from each focal group was observed for a total of 10 min in the morning (0800–1200) and 10 minutes in the afternoon (1300–1800). During these focal watches, all behaviors exhibited were recorded on plastic slates (for a detailed recent ethogram of the behavioral repertoire of this species, see Sopinka et al. 2009). Specifically, we recorded the occurrence of aggressive acts (bites, chases, rams, and aggressive displays), submissive acts (submissive displays and postures), and care (digging, carrying, defense against hetero- and conspecifics, and brood chamber visits). In addition, the time (seconds) that any of the focal individuals was away from their territory was recorded using a stopwatch. Following focal observations, for the 11 groups assigned to the removal treatment, the nonfocal breeder females and her associated helpers were collected. This produced 11 "experimentally monogamous" (EM) groups since only the focal group including the previously polygynous breeder male remained. We also removed the rocks belonging to the nonfocal group (females and helpers) to prevent settling of other new individuals near the focal group. The removed fish were brought to the surface where they were used in another concurrent experiment.

The next day (Day 1), behavioral watches were conducted on all focal individuals in each focal group from both the removal and control treatments as described for Day 0. Behavioral watches were repeated 5 days postmanipulation (Day 5) and 9 days postmanipulation (Day 9). For $N = 3$ control and $N = 3$ removal groups, one or more focal fish could not be relocated by Day 9, therefore these groups were excluded from analyses of behavior.

Following Day 9 observations, all focal individuals were collected, brought to the surface, measured (SL to the nearest 1 mm and weight to the nearest 0.1 g) and quickly euthanized by giving them a firm cephalic blow followed by decapitation. Within 60 s, a blood sample was taken by caudal severance and blood drawn using heparinised microcapillary tubes. Blood collected was spun at 8000 ? *g* for 10 min in a mini centrifuge, and the separated plasma removed and stored at −20 °C. The blood plasma samples were transported back to McMaster University, Canada at −4 °C for hormone assay and stored at −20 °C for later analysis of 11KT and T concentrations.

Steroid hormones were extracted using an ether extraction procedure previously optimized and used for this species (Desjardins et al. 2006, Desjardins, Fitzpatrick, et al. 2008; Taves et al. 2009). Sufficient plasma was collected for EM ($N = 7$) and NP ($N = 8$) breeder males and EM ($N = 6$) and NP ($N = 7$) breeder females. We determined the concentrations of 11KT in males and T in females using available commercial EIA kits (Cayman Chemical #582701 and 582751, Ann Arbor, MI) as per the manufacturer's instructions. Each hormone was assayed in duplicate with a final dilution of plasma of 1:300 for 11KT and 1:150 for T. The reported hormone levels are average concentrations calculated from duplicate aliquots whose values fell within the 20–80% binding limits (B/B_0) of the appropriate standard curve following a log–logit transformation, corrected for average hormone recovery factors of 81.3 ± 0.02% for 11KT and 87.8 ± 0.03% for T based on a cold-spike method. Average inter- and intra-assay coefficient of variation for 11KT was 7.9 ± 4.7% and 7.6 ± 1.8%, respectively, and average intra-assay coefficient of variation for T was 16.1 ± 3.4%. No inter-assay coefficient of variation was calculated because all plasma T samples were run on the same assay. The assays for T and 11KT have been validated previously for this species (Desjardins et al. 2006).

Ten naturally monogamous (NM) groups were also located from the same field site and the breeding male collected to enable comparisons of age and size between NM and polygynous groups. The body of each collected individual was measured, dissected, and the brain, gonads, and liver individually weighed. Gonadal investment for each individual was calculated using the gonadosomatic index (GSI = mass of the gonads/mass of the soma [body mass − the gonad mass] × 100). Age was also determined because age could also influence competitive ability and size and age can be decoupled in fish owing to social and/or environmental modulation of growth. To determine age, otoliths (or ear bones) were removed from the otic cavity, cleaned, and allowed to dry. A thin transverse section of each otolith was prepared using standard methodology (for details, see Choat and Axe 1996). The thin section was viewed with a light microscope and the number of light–dark increments counted. The structure of the otolith increments matched that seen in many other species of fish where otolith increments have been validated as annual (Choat and Robertson 2002), therefore each increment was assumed to represent 1 year of age.

Do breeder males and females prefer larger partners?

A forced choice experiment was conducted between 12 September 2005 and 16 January 2006 at McMaster University in Hamilton, Canada. Breeder males ($N = 11$) or breeder females ($N = 11$) (SL > 4 cm) were placed into a 3-chambered T-shaped tank (41 × 21 × 26 cm) where fish could associate with either a larger or smaller stimulus fish of the opposite sex (Figure 1). The 2 stimulus fish were placed on either side of an opaque barrier, to prevent them from seeing each other. Both could be viewed by the choosing fish across a transparent barrier. The stimulus fish differed in size from each other by between 5.1–9.7 mm for males and 5.1–9.9 mm for females. Fish were habituated to the choice tank for 3 hours during which the tank was kept dark to decrease the stress experienced following capture and removal from their social groups. A temporary opaque barrier was also placed between the focal fish and the 2 stimulus fish during this first phase. When the first phase habituation period was completed, the black bag was removed and the fish experienced the second-phase habituation period (in test tank with light) for 10 min. After the second-phase habituation period, a side preference control period began. With the temporary opaque barrier still in place between the focal fish and the 2 stimulus fish, the amount of time the focal fish spent on either side of the tank was recorded for 2 min. Following the control period, the trial period commenced with the temporary opaque barrier between the focal fish and the 2 stimulus fish being removed, allowing the focal fish to view both stimulus fish for a 10 min period. The amount of time that the focal fish spent with either stimulus fish was recorded for each of the twenty 10 min trials. In addition, all social behavior and activity levels of both focal and stimulus fish were recorded (Sopinka et al. 2009). The preferred stimulus fish was defined as the one that the focal fish spent more than half of the trial time associating with. Following the trial, all fish were returned to their original social groups. Each trial used a unique set of stimulus fish, and the side where the bigger versus smaller stimulus fish was placed was counterbalanced across trials. We used 2 different preference measures (time associating with large vs. small males and the frequency of preference for each type of male) because both metrics are commonly used in studies of mate choice.

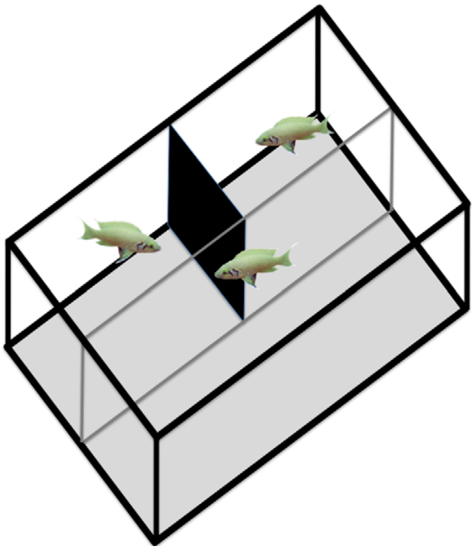

Figure 1
Forced choice 3-chambered T tank.

Statistical analyses

All data were checked for normality and homogeneity of variances. Data that were not normally distributed were log transformed and parametric tests employed. To compare the distances to nearest neighbours between polygynous and monogamous groups, we used a 2-sample randomization t-test (RUNDOM Pro 3.14; Jadwiszczak 2002) because nearest neighbor distances between 2 polygynous groups within a single male's harem were not independent of each other (Stiver et al. 2004). A two-sample randomization t-test was also used to compare the relatedness between nearest neighbor females for polygynous versus monogamous groups to control for nonindependence of pairwise relatedness values between polygynous females in a harem. To compare relatedness between individuals in monogamous versus polygynous groups, two-sample randomization tests were used to control for nonindependence of data, since each group member was tested for multiple pairwise relatedness values. Standard t-tests were used to compare the pairwise relatedness between breeders in monogamous versus polygynous groups as there was only 1 breeding pair per group. For the experimental manipulation of the mating system, we used General Linear Models (GLM) to assess changes in the frequency of behaviors expressed by each focal individual over time in the 2 treatments. Treatment (control vs. removal) and subpopulation were entered as categorical predictor variables and the average change in the frequency of behavior was entered as the response variable. Since there were no differences in frequencies of any behaviors between Day 1, Day 5, and Day 9 (analysis of variance: all behaviors, $P > 0.05$), the 3 postmanipulation measurements were averaged, and change in behavior calculated as: (average postmanipulation frequency) − (premanipulation frequency). To determine whether males and females preferentially associated with larger or smaller members of the opposite sex in the mate choice experiment, we compared the frequency with which focal fish chose the larger or smaller stimulus fish using chi-square tests, and compared the average time spent with larger or smaller stimulus fish with paired t-tests.

Ethics

All fish handling and experimental procedures used were reviewed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol # 06-10-59) and adhered to the animal handling guidelines specified by the Canadian Council for Animal Care.

RESULTS

Does the EPP explain the variable mating system?

On average, the territories of 2 polygynous groups within the same harem were more closely clustered (0.88 ± 0.06 m) than were the territories of monogamous groups to their nearest conspecific neighbors (2.61 ± 0.27 m) (Randomized *t*-test: $t = 1.74$, $P < 0.001$; Figure 2a). The average relatedness between breeder females and their nearest neighboring breeder female did not differ between polygynous ($r = 0.012 \pm 0.029$) and monogamous groups (0.037 ± 0.036) (Randomized *t*-test: $t = 0.025$, $P = 0.59$; Figure 2b).

Polygynous breeder males (5.93 ± 0.03 cm, $n = 72$) were significantly larger than monogamous breeder males (5.80 ± 0.04 cm, $n = 61$) (*t*-test: $t = 2.32$, $P = 0.02$), and had larger gonads than monogamous males (analysis of covariance [ANCOVA]: $F_{1,117} = 11.2$, $P = 0.001$). There was a positive relationship between male body size and age (Pearson's correlation: $R = 0.74$, $n = 27$, $P < 0.001$). After controlling for body size, monogamous and polygynous males did not differ in age (GLM: $F_{1,24} = 1.54$, $P = 0.23$). Female breeder size was positively correlated with male breeder size in both monogamous ($R = 0.5$, $n = 51$, $P < 0.001$) and polygynous groups ($R = 0.4$, $n = 63$, $P = 0.001$). Even so, breeder females in polygynous groups were not significantly larger (5.14 ± 0.04 cm, $n = 63$) than those in monogamous groups (5.15 ± 0.05 cm, $n = 51$) ($t = 0.15$, $P = 0.88$). Helpers in polygynous groups ($n = 258$) were significantly larger (4.18 ± 0.06 cm, $n = 258$) than helpers in monogamous groups on average (3.65 ± 0.06 cm, $n = 286$) ($t = 5.92$, $P < 0.001$). Helpers in polygynous groups were still larger than those in monogamous groups after controlling for breeder male size in polygynous and monogamous groups (ANCOVA: $F_{1,448} = 21.2$, $P < 0.001$). Incorporating breeder male size controls for the influence of strategic growth regulation on helper size (Heg, Bender, et al. 2004).

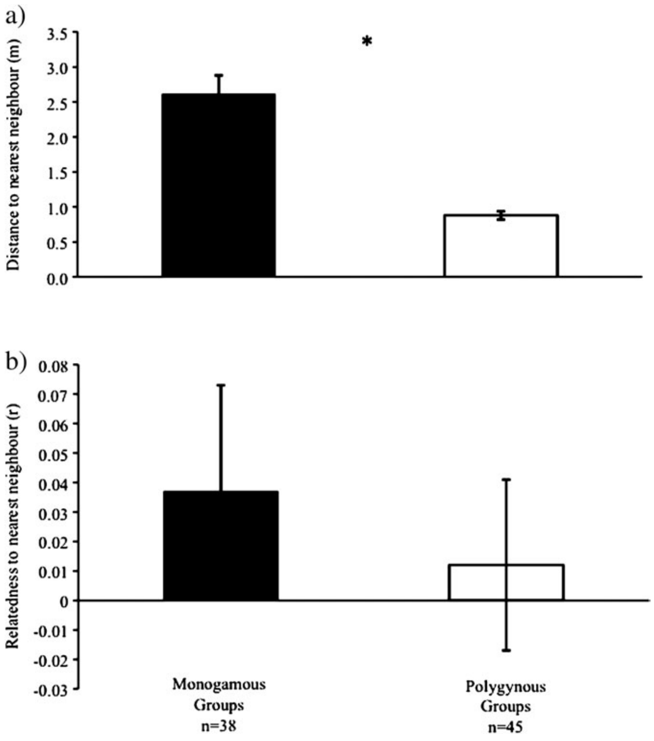

Figure 2
Assessment of EPP model predictions. (*A*) Average distance (m) between monogamous and polygynous groups and their nearest neighbor, and (*B*) average relatedness (*r*) between monogamous and polygynous breeder females and their nearest neighboring breeder female.

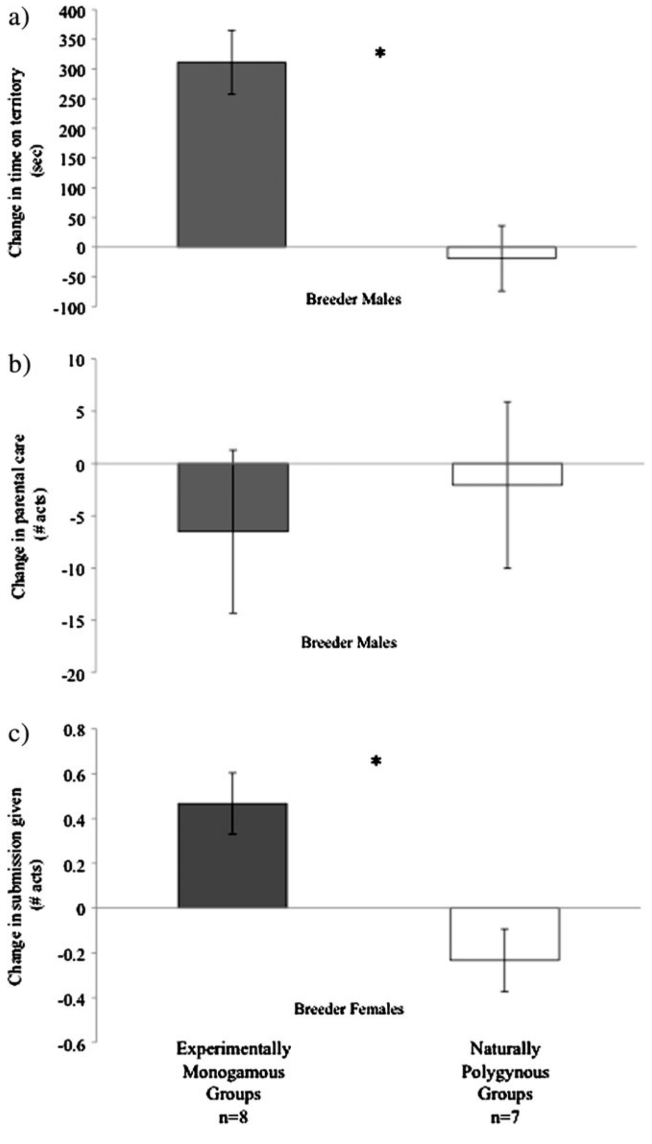

Figure 3
Behavioral changes of breeder males and females in response to mating system manipulation. (*A*) Average change in time spent (in seconds) on the focal territory, (*B*) average change in parental care (number of acts performed on the focal territory) for breeder males in EM and NP treatments, and (*C*) average change in submission given by breeder females to breeder males (number of acts performed on the focal territory) in EM and NP treatments. Positive values indicate an increase in the time spent or number of acts performed after (average of Day 1, 5, and 9) relative to before (Day 0) mating system manipulation and negative values indicate a reduction in the time spent or number of acts performed after (average of day 1, 5, and 9) relative to before (Day 0) mating system manipulation.

Does sexual conflict between breeders influence the mating system?

Breeder males

EM males ($n = 8$) spent significantly more time on their remaining territory than did NP males ($n = 7$) following the experimental manipulation (GLM: $F_{1,5} = 18.4$, $P = 0.008$; Figure 3a). Additionally, immediately after becoming EM (Day 1), males with large gonadal investment (high GSIs) spent less time on their territories than those with low investment ($R = -0.95$, $P < 0.001$). EM males did not perform more parental care than NP males ($F_{1,5} = 1.5$, $P = 0.28$). When controlling for time on territory, EM males still did not perform more acts of parental care on their territory than NP males ($F_{1,4} = 2.9$, $P = 0.19$; Figure 3b). EM breeder males were not more aggressive toward their remaining breeder females than were NP males ($F_{1,4} = 4.0$, $P = 0.11$). EM and NP males did not differ in the concentration of 11KT found in their plasma (EM: 7.5 ± 1.7 ng/ml; NP: 6.9 ± 1.6 ng/ml, $F_{1,13} = 0.06$, $P = 0.81$). Among EM males, those that spent less time on their territories tended to have higher 11KT levels than those that spent more time on their territories ($R = -0.72$, $n = 7$, $P = 0.07$). There was no such trend among NP males ($R = 0.05$, $n = 8$, $P = 0.9$).

Breeder females

Following experimental manipulation, females paired with EM males spent the same amount of time on their territories ($F_{1,5} = 1.9$, $P = 0.23$) and performed the same amount of parental care ($F_{1,5} = 0.13$, $P = 0.74$) as females paired with NP males. However, females paired with EM males became significantly more submissive toward their mates than females paired with NP males postmanipulation ($F_{1,5} = 12.8$, $P = 0.02$; Figure 3c). This difference did not hold after controlling for the time males spent on their territories (ANCOVA: $F_{1,4} = 8.02$, $P = 0.42$), indicating that the increased levels of submission by EM females arises because EM males spend more time on their territories. Levels of plasma T were also not significantly different between females in the EM groups (3.6 ± 2.1 ng/ml) and the NP groups (4.8 ± 1.9 ng/ml) ($F_{1,11} = 0.17$, $P = 0.69$).

Helpers

Following the manipulation, helpers in EM and NP groups spent similar amounts of time on their territories (GLM: $F_{1,18} = 1.4$, $P = 0.25$). There was also no difference in the amount of alloparental care provided by helpers in EM and NP groups ($F_{1,18} = 0.001$, $P = 0.98$) or in other social behaviors ($F_{1,18} = 0.04$, $P = 0.85$). Neither helper body size nor helper sex accounted for significant variation in time they spent on the territory (size: $F_{1,18} = 3.18$, $P = 0.09$; sex: $F_{1,18} = 1.76$, $P = 0.2$) or the frequency of alloparental care they performed (size; $F_{1,18} = 0.12$, $P = 0.89$; sex: $F_{1,18} = 0.13$, $P = 0.73$). The fact that helpers in the EM and NP groups behaved similarly indicates that the removal of rocks during the EM manipulation was not likely to be the cause of changes in the behaviors of breeders.

Do male and female *N. pulcher* prefer larger mates?

Females and males showed no particular side preference prior to seeing the stimulus fish (females: $\chi_1^2 = 0.18$, $P = 0.67$; males: $\chi_1^2 = 1.64$, $P = 0.20$) nor did they spend more time on any particular side of the choice tank (females: $t = 0.06$, 0.96; males: $t = 0.84$, $P = 0.42$). During the choice trials, focal females more often associated with the smaller stimulus male than the larger stimulus male ($\chi_1^2 = 4.6$, $P = 0.03$; Figure 4), whereas focal males showed no preference for associating with either smaller or larger stimulus females ($\chi_1^2 = 1.64$, $P = 0.2$). There was no difference in the amount of time focal females or males spent with the smaller or larger stimulus fish (Paired t-test: females, $t = 1.16$, $P = 0.26$; males, $t = 0.98$, $P = 0.35$). A post hoc power analysis revealed that the power to detect a significant difference in time spent associating was moderate ($P = 0.48$).

Does mating behavior influence levels of cooperation by helpers?

There was no difference in the average pairwise relatedness between breeders in monogamous ($r = 0.12 \pm 0.03$) and polygynous groups (0.08 ± 0.02) (randomized t-test: $t = 0.04$, $P = 0.34$). However, average helper relatedness to both breeders was greater in monogamous (0.08 ± 0.01) than in polygynous groups (0.008 ± 0.01) ($t = 0.07$, $P < 0.001$; Figure 5a). This pattern was driven by both increased relatedness to breeder males and females separately ($P < 0.01$ for both). Helpers were also more closely related to each other in monogamous (0.16 ± 0.01) than in polygynous groups (0.07 ± 0.01) ($t = 0.09$, $P = 0.0001$; Figure 5b). In spite of this, they did not help more in monogamous compared with polygynous groups (GLM: $F_{1,75} = 0.01$, $P = 0.91$; Figure 5c).

DISCUSSION

Since the seminal work of Emlen and Oring (1977), variation in mating systems has been viewed as a consequence of resource and hence female dispersion (Kleiman 1977; Rutberg

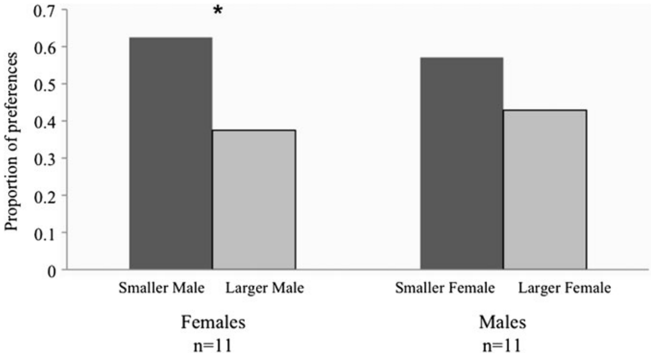

Figure 4
Mate preferences of males and females. Proportion of preferences for smaller (dark gray) versus larger (light gray) opposite sex stimulus fish for focal breeder females ($N = 11$) and breeder males ($N = 11$).

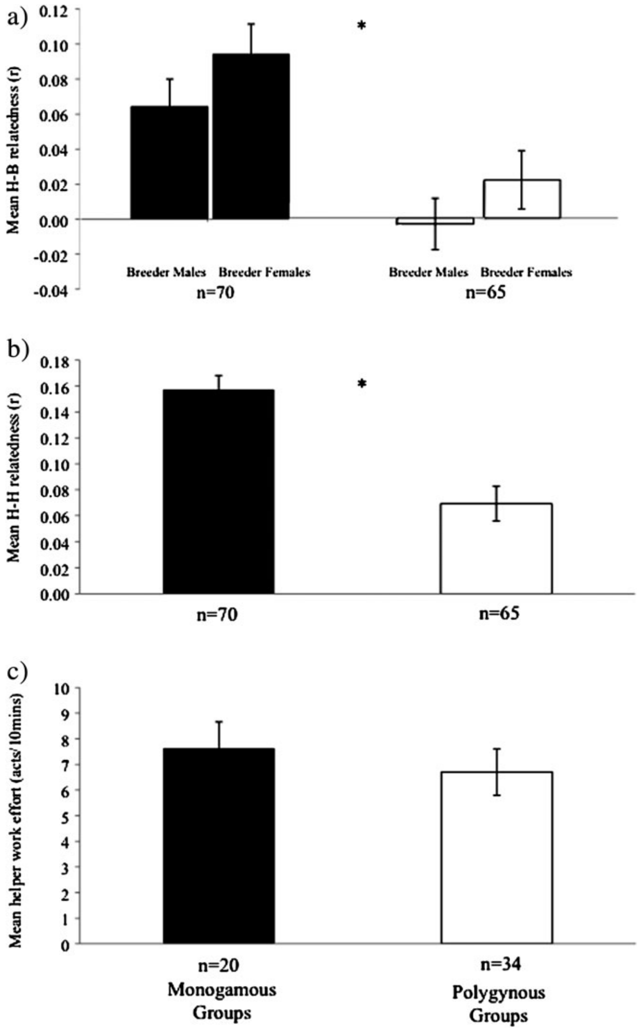

Figure 5
Relationships between mating systems, relatedness, and helping. (*A*) Average relatedness between helpers and breeder males or females, (*B*) average relatedness between helpers, and (*C*) average work effort by helpers, in monogamous versus polygynous groups.

1983; Vehrencamp and Bradbury 1984; Clutton-Brock 1989; Davies 1991; Travis et al. 1995). For *N. pulcher*, which exhibits a variable mating system, monogamy occurred when females were dispersed and polygyny when females were clumped, supporting the EPP model. Additionally, polygynous males were larger and had larger gonads than monogamous males, suggesting that large males are better able to monopolize multiple females and enjoy a mating advantage (Desjardins, Fitzpatrick, et al. 2008). Although male body size and age were positively correlated, age was not a significant predictor of the mating system when controlling for size, suggesting that it is body size per se that determines the mating system males can achieve. Relatedness to the nearest neighboring female was similar for monogamous and polygynous females, suggesting that female spatial distribution, and hence the mating system, is not determined by preferential kin associations among females. It is also unlikely that a heterogeneous food distribution promotes female clumping and polygyny in this species, since *N. pulcher* feed on planktonic food resources (Kondo 1986; Gashagaza 1988), which have only been shown to vary on extremely large spatial scales (Kurki et al. 1999). Instead, the most important determinant of female dispersion in *N. pulcher* is likely to be the distribution of rocks, since rocks serve as shelters which are a crucial resource for protecting group members from predators (Balshine et al. 2001; Heg, Bachar, et al. 2004) and enabling breeding (Taborsky and Limberger 1981).

While ecological factors like the distribution of food and shelters may predispose certain mating systems to arise, sexual conflict has the potential to modulate the actual mating systems observed (Davies 1985; Reynolds 1996). In *N. pulcher*, females face an apparent trade-off between male care and quality that is related to the mating system. When monogamous, females settle with a small low-quality male that provides more care, and when polygynous, females settle with a large high-quality male that provides less care. Interestingly, our experiment showed that females mated monogamously with large high-quality males are unlikely to have the "best of both worlds," since females in EM groups performed more acts of submission toward males which is known to be energetically costly (Grantner and Taborsky 1998; Taborsky and Grantner 1998). Since these large males did not direct more aggression toward females, the submission by females may preempt any increased aggression from males (Bergmüller and Taborsky 2005). Furthermore, the fact that large males did not perform more acts of care when made EM compared with when NP suggests that the additional submission cost for females would not be compensated by the usual benefits that females accrue from increased paternal care under monogamy. It is important to note that securing a male's assistance in territory defense, maintenance, and broodcare is likely to be advantageous for females given that breeder males provide as much care as helpers on average (Desjardins, Stiver, et al. 2008). Thus, contrary to initial expectations, the cost of mating monogamously with a large dominant male may serve to mitigate sexual conflict, and result in a system where females are equally likely to accept monogamy with a small male or polygyny with a large male, as is observed in natural populations (Desjardins, Fitzpatrick, et al. 2008).

In other species, costs to females of mating with dominant males have also been reported (Jennions and Petrie 1997; Qvanström and Forsgren 1998; Beehner et al. 2005). For *N. pulcher*, this also appears to be the case but only if the mating system is monogamous. Indeed, results of our laboratory choice test indicate that females do not prefer to mate with the larger of two unmated males and hence may incur a cost from mating monogamously with large males. It should be noted here that the 2 analyses of preference, one based on final preference outcome and the other based on time spent with each fish, indicated either a preference for smaller males or no preference, respectively. While these interpretations are not aligned in terms of significance, they are aligned in terms of a lack of preference for larger males. Interestingly, this lack of preference for large males is contradictory to the polygyny threshold model (Orians 1969), which states that females should choose to mate with a larger, high quality male unless that male is already mated. Additional female choice tests in which the mating status and the relative size of stimulus males are simultaneously manipulated, combined with assessments of fitness-related consequences of these different mating options for females, would be an important next step to test these predictions of female preferences.

From the male's perspective, polygyny is generally thought to yield the greatest net benefit since males have a higher potential reproductive rate than females and can enhance their mating success by mating multiply (Clutton-Brock and Vincent 1991). This appears to be the case for *N. pulcher*, whereby polygynous males have a higher reproductive success, in terms of total number of surviving offspring, than monogamous males (Desjardins, Fitzpatrick, et al. 2008). Small monogamous males are therefore likely to be making the best of a bad situation until they become large and competitive enough to maintain a polygynous harem. In addition, males are expected to exhibit preferences for highly fecund females (Andersson 1994; Kraak and Bakker 1998; Dosen and Montgomerie 2004; Werner and Lotem 2005), which is often correlated with body size in fishes (Bagenal 1967). However, the mate choice experiment demonstrated that *N. pulcher* males exhibited no obvious size preference. *Neolamprologus pulcher* males may have shown no size-related female preferences because in this species, breeding spots are rare and male reproductive success is much more likely to be impacted by their capacity to hold on to a breeding territory than via choice of a particularly large female mate. This lack of preference for size also indicates that the positive correlation between breeder male and female size within pairs is not likely to be a consequence of active size-assortative pairing. Instead, size-matched pairing could be a result of cooperative growth regulation between pairs, as has been demonstrated for a coral goby (*Gobiodon histrio*; Munday et al. 2006), or more simply arise due to differential access to food between groups (Madsen and Shine 2000; Buston and Elith 2011).

Small monogamous males naturally have lower levels of 11KT than large polygynous males (Desjardins, Fitzpatrick, et al. 2008). The fact that EM males did not exhibit lower levels of plasma 11KT after 9 days relative to NP males demonstrates that EM males remained physiologically (and behaviorally) "polygynous" despite becoming socially monogamous, and suggests that elevated levels of 11KT may be a cause rather than a consequence of a polygynous mating system. The high 11KT in EM males may be related to the low levels of parental care by EM males, supporting the reported trade-off between parental care and 11-KT mediated dominance behaviors (Hegner and Wingfield 1987; Ketterson and Nolan 1992; Reburn and Wynne-Edwards 1999; Ros et al. 2004; Desjardins, Fitzpatrick, et al. 2008). Breeder females in EM and NP groups also showed no differences in the levels of T or care exhibited, which corroborates the lack of change in parental care they provided under the 2 treatments. Future work examining changes in levels of cortisol in females in the 2 treatment groups would potentially shed light on more subtle consequences and costs of mating systems for females, as conducted in other animal societies (e.g., Beehner et al. 2005), particularly owing to the potential stress of submissive appeasement for females under EM.

In other cooperative breeders, helpers have been shown to influence reproductive options of breeders by compensating for any reductions in parental care (Mulder et al. 1994; Green et al. 1995; Webster et al. 2004). In *N. pulcher*, where polygynous males typically provide less help than monogamous males (Desjardins, Fitzpatrick, et al. 2008), helpers might therefore be expected to be more helpful in polygynous groups if they compensate for reductions in parental care. However, helpers exhibited no change in helping effort under EM compared with NP, and helpers in NM groups provide similar amounts of care as those in NP groups (Desjardins, Fitzpatrick, et al. 2008). Furthermore, when helpers were experimentally removed in the field, remaining large helpers did not increase levels of help (Brouwer et al. 2005). These results together suggest that, unlike some other cooperative breeders, *N. pulcher* helpers do not compensate for reductions in help of other group members, and as such, may not influence the payoffs from monogamy versus polygyny for breeders. However, direct tests of this hypothesis are now required, for example, by manipulating levels of help provided by helpers and comparing the behavioral responses of breeders in monogamous and polygynous groups.

Relatedness between group members was greater in monogamous compared with polygynous groups. This pattern could arise if the degree of dispersal to and from dispersed monogamous groups is reduced relative to clustered polygynous groups, if breeder turnover is reduced in monogamous relative to polygynous groups, or if there is more mixed parentage in polygynous groups, all explanations requiring further testing. Despite the relatively higher relatedness in monogamous groups, helpers did not provide more alloparental care. This suggests that while relatedness may influence cooperation in some situations (e.g., Stiver et al. 2005; Wong and Balshine 2011), the low average relatedness in the current study makes it unlikely that kin selection per se would specifically play a role in any cooperation differences between monogamous versus polygynous groups.

In conclusion, we have shown that the mating systems of *N. pulcher* are a result of resource distribution combined with male–male competition and the mitigation of sexual conflict. Contrary to expectations, experimental manipulation of the mating system revealed a hidden cost of monogamy for females in the form of increased submission toward large dominant males, which in turn, challenges the widely held assumption that the presence of other females within a harem is always costly for females. This additional cost of monogamy with a large male is likely to render polygyny with a large male and monogamy with a small male (the observed mating systems) more profitable for females, thus reducing the intensity of sexual conflict over the mating system.

FUNDING

Dr Marian Wong was supported by postdoctoral fellowships from the Association of Commonwealth Universities and Ministry of Research and Innovation Ontario. The funding for this research project was a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada (RGPIN222854-11) awarded to Dr Sigal Balshine.

We thank John, Enoch, and Maxwell Juma for their untiring help in the field, and Bornfirst and family for running the day-to-day operations of Tanganyika Lodge. We thank Drs Harris Phiri, Patrick Nagalda, and Justina Kasabila of the Zambian Ministry of Agriculture, Food and Fisheries, as well as Rueben Shappola and the Department of Fisheries, in Mpulungu for their logistical support of research. We thank Louise Stanley for otolith microchemistry, Kathleen Sharland for performing choice tests, Denys DeCatanzaro for use of his plate reader, Jordan Brown-Marsh for his assistance with the figures, and Adam Reddon, Peter Buston, and Nathan Osborne for helpful comments on the manuscript. All research was approved by Animal Research and Ethics Board at McMaster University (06-10-59) and conformed to guidelines of the Canadian Council on Animal Care.

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