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Original Article

Polygyny affects paternal care, but not survival, pair stability, and group tenure in a cooperative cichlid

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It is generally assumed that there is sexual conflict over the mating system. In this view, polygyny benefits males at a cost to females, and it is hence unclear why females accept polygynous mating. However, in the facultatively polygynous fish, *Neolamprologus pulcher*, no costs of polygyny to females have thus far been detected. We hypothesized that the costs of polygyny remained undetected because they accrue over longer periods of time through reduced tenure and/or survival. We conducted an extended field study in which we monitored the behavior and survival of individuals breeding either monogamously or under polygynous conditions within the same natural colony. We expected that polygyny would reduce male and female survival through increased competition among males and reduced amounts of received paternal effort for females. Consequently, breeder tenure and pair stability were predicted to be lower in more polygynous groups. Our data indeed revealed costs of polygyny to both sexes. Polygynous males faced higher competition, and females paired to polygynous males received reduced paternal effort. However, this did not result in different survival rates between individuals breeding under monogamous or polygynous conditions. We conclude that in *N. pulcher* the fitness costs of polygyny may be either too marginal to be detected with the approaches used thus far, or that males and females in this species do not face a conflict of interest over the mating system. This raises the question which ecological factors may resolve sexual conflict, and how the accruing mating system feeds back on a species' ecology.

Key words: cichlid, cooperation, kin selection, parental care, polygamy, sexual conflict.

INTRODUCTION

Mating systems have received considerable attention from evolutionary biologists because of the central role of sexual reproduction for the evolution of biological diversity. Unraveling how mating systems are shaped by selection and how mating systems in turn shape selective pressures is crucial for an understanding of evolutionary processes (Shuster and Wade 2003). Most notably, the comparison of sex-specific costs and benefits of different mating systems can provide insight into important evolutionary processes; sexual conflict, mate choice, assortative mating, and related phenomena have been identified as important components of diversification and speciation (Bolnick and Fitzpatrick 2007; Ritchie 2007; Maan and Seehausen 2011).

A widespread and intensely studied mating system is polygyny, where a single male is paired with more than 1 female (Shuster and Wade 2003). Polygyny is generally expected to impose costs to females, especially in species where males participate in offspring

care (Emlen and Oring 1977; Shuster and Wade 2003). This is because males that divide their paternal investment between several females are likely to afford a reduced amount of investment to each of their mates, compared with monogamous males (Webster 1991; Slagsvold and Lifjeld 1994). Males, on the other hand, are expected to gain from polygyny because mating with more females typically increases the number of offspring they have (Bateman 1948; Emlen and Oring 1977; Shuster and Wade 2003). Thus, the potential conflict of interest between the sexes may be particularly apparent in polygynous species (Chapman et al. 2003; Shuster and Wade 2003).

Interestingly, polygyny is often facultative and co-occurs with monogamy in a species or population (Clutton-Brock 1989). Here, the crucial questions are why some females accept polygynous mates and what allows some males to mate with several females, while other individuals mate monogamously. Different explanations for 1) how females may receive compensation for the costs of polygynous mating, 2) how males may differ in their ability to mate polygynously, and 3) how sexual conflict may be resolved, have been proposed: a) Only high quality males may be able to

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mate polygynously (Shuster and Wade 2003) and females mated with such males may thus benefit from “good genes” or “sexy sons” (Weatherhead and Robertson 1979; Neff and Pitcher 2005) or b) polygyny may be “the best of a bad job” for lower quality females (Grønstøl et al. 2003). To test these hypotheses, it is important to know what the costs and benefits of polygyny really are.

Most research on facultatively polygynous species has been conducted on birds, especially on great reed warblers (Catchpole et al. 1985) and European starlings (Pinxten et al. 1989). Here, provisioning rates are typically interpreted as parental effort while survival of chicks to independence is interpreted as reproductive success and a proxy of fitness (e.g., Bensch 1996; Sandell et al. 1996). Thus, reduced male provisioning, which often results in reduced offspring survival, constitutes the major cost of polygyny to females, whereas increased total numbers of surviving offspring are the major benefit to polygynous males (Webster 1991). Consequently, there is an apparent conflict between the sexes over the mating system: Females should prefer monogamy, whereas males should prefer polygyny (Shuster and Wade 2003). Typically, these factors are measured for a single breeding season only, and lifetime effects of polygyny are not often reported. It has been shown, however, that some costs and benefits of polygyny may only be detected in long-term studies (Hasselquist 1998; Huk and Winkel 2006).

Another system in which the consequences of facultative polygyny have been investigated is the cooperatively breeding cichlid fish *Neolamprologus pulcher* (Taborsky and Limberger 1981). In this species, breeding takes place in territories defended by groups in which a dominant breeder pair largely monopolizes reproduction (see Methods for a more detailed description of the species). Although a considerable proportion of males breeds in only 1 group, hence being monogamous, males may be mated with up to 6 females simultaneously (Limberger 1983; Desjardins, Fitzpatrick, et al. 2008). In *N. pulcher*, polygyny has been shown to be beneficial to males due to increased numbers of offspring produced and to reduce the paternal care that females and their offspring receive (Limberger 1983; Desjardins, Fitzpatrick, et al. 2008; Wong et al. 2012). Interestingly, the reduction in received male care effort appears to have no negative short-term effect on female fitness (Desjardins, Fitzpatrick, et al. 2008). Rather, because polygyny appears to be limited by male–male competition and only large, high quality males seem to be able to defend several breeding territories, females may gain from polygyny through “good genes” and reduced received aggression from their mate (Wong et al. 2012). Yet, it is possible that the costs of polygyny to females accrue over longer periods of time, for example through reduced survival. Furthermore, the costs of intrasexual competition for males and how these costs may vary between monogamous and polygynous individuals has not yet been studied in this species. For instance, polygyny may affect survival in a way that males defending more territories suffer from a shortened lifespan.

The potential influence of polygyny on survival of *N. pulcher* is especially interesting because the fish engage in cooperative breeding. The evolution of cooperative behavior, that is, an individual accepting a cost at another’s benefit, is somewhat paradoxical (West et al. 2007). It can however be explained if cooperation increases an individual’s direct fitness (e.g., via delayed benefits: Taborsky 2013; Kingma et al. 2014) or if it is directed toward related individuals, thus increasing the cooperator’s indirect fitness (Hamilton 1964; Lehmann and Keller 2006). Monogamy leads to higher relatedness among potentially cooperating individuals compared with polygamy and has thus been argued to be an important precondition for

the evolution of cooperation (Boomsma 2013). Indeed, monogamous mating appears to be linked to the evolution of cooperative breeding in insects (Hughes et al. 2008), birds (Cornwallis et al. 2010), and mammals (Lukas and Clutton-Brock 2012). In *N. pulcher*, mating is largely monogamous for a given clutch, but groups consist of individuals from different clutches that may considerably vary in age (see Methods for details). Thus, if polygyny affected breeder tenure, it would also affect within-group relatedness, with potential consequences for the costs and benefits of cooperative breeding. A lower relatedness among subordinates and between subordinates and dominants has indeed been found in polygynous compared with monogamous groups of this species (Wong et al. 2012). Although this study did not find any differences in cooperative behavior of subordinates in monogamous and polygynous groups, other work has shown that relatedness may indeed influence cooperation in these fish, albeit in direct brood care which cannot be measured in the field (Zöttl et al. 2013).

To unravel whether polygyny is costly to males and/or females of *N. pulcher* over longer periods of time, we measured behavioral differences between males defending different numbers of breeding territories in the same natural colony. In the subsequent year, we checked in the same colony which of the individually marked breeders had survived. We hypothesized that 1) males defending more breeding territories would face higher competition and/or would bear other costs (e.g., reduced feeding, increased predation risk, increased paternal effort), 2) higher competition and/or other costs would reduce male survival and tenure times, 3) females paired with males defending more breeding territories would receive less paternal care, and 4) reduced received paternal care would in turn reduce female survival and tenure. Consequently, we expected 5) pair-bonds to be shortened if males defended more breeding territories, resulting in 6) groups experiencing higher breeder turnover if their respective dominant male defended more breeding territories. This would ultimately reduce relatedness between breeders, subordinates, and dependent offspring, thus reducing the indirect fitness gains of group members in polygynous groups. The assumed costs of polygyny would highlight potential conflicts between males and females over the mating system that remained undetected in studies conducted over shorter time periods.

METHODS

Study species and general field methods

Neolamprologus pulcher is a cooperatively breeding cichlid fish endemic to Lake Tanganyika, East Africa (Duftner et al. 2007). The fish form breeding groups composed of a dominant breeder pair and several subordinate brood care helpers of both sexes and of varying age and size (Taborsky and Limberger 1981; Balshine et al. 2001). Groups defend territories against foreign conspecifics and heterospecifics, in which group members find shelters for protection from predators and for breeding (Balshine et al. 2001; Desjardins, Fitzpatrick, et al. 2008). Individuals are typically tolerated in 1 group only, that is, in their respective home territory, but large males can defend the dominant position in more than 1 breeding group (Limberger 1983; Desjardins, Fitzpatrick, et al. 2008; Wong et al. 2012). Groups typically cluster in colonies of a few up to more than 100 groups in close vicinity (Heg et al. 2008). Reproduction within groups is largely monopolized by the dominant breeder pair, but some extrapair reproduction has been recorded (e.g., Dierkes et al. 2008; Stiver et al. 2009; Hellmann et al. 2015; summarized in Taborsky 2016). Breeder turnover appears to be frequent and

even more so in males than in females (Dierkes et al. 2005; Stiver et al. 2006).

We studied a natural colony of *N. pulcher* located off the Zambian coast of Lake Tanganyika, at Kasakalawe Point near Mpulungu (8°46.849'S, 31°04.882'E; Jungwirth et al. 2015). The focal colony covered an area of approximately 30 by 30 meters at a depth of 10–12 m, and we marked and mapped all territories of *N. pulcher* breeding groups found in the colony. For each breeding group, we recorded 1) its size (as the number of individuals larger than 1.5-cm standard length (SL) to the nearest millimeter; cf., Heg and Taborsky 2010), 2) its recent reproductive output (as the number of juvenile fish smaller than 1.5-cm SL, not counting larvae or fry), 3) its distance to the nearest neighboring group (from territory center to territory center; calculated based on territory positions), and 4) whether its respective dominant male defended the breeder position also in other groups.

Colony characteristics and selection of focal individuals

In 2012, the focal colony consisted of 146 territories, each supporting a breeding group. A total of 78 males defended the dominant breeder position in these territories. Of these males, 34 defended a single territory, 27 defended 2 territories, 14 defended 3 territories, and 1 male each defended 4, 5, and 6 territories, respectively. We selected 37 individual dominant males as focal individuals for this study: 11 with 1 breeding territory, 14 with 2 territories, 9 with 3 territories, and 1 male each with 4, 5, and 6 territories, respectively (resulting in 81 breeding territories being considered in this study). Males were selected by the following criteria: 1) the territories were easily accessible and observable without disturbing other groups (thus, some males in very dense areas of the colony were excluded), 2) the respective breeding groups were not particularly small (smaller groups are more likely to go extinct [Heg et al. 2005] and we aimed to not increase extinction risk by disturbance through catching and observing; thus, some males with very small groups were excluded), and 3) we aimed to cover a broad range of local colony densities (average nearest neighbor distance in the whole colony: 0.72 m, range: 0.16–3.18 m; average nearest neighbor distance of the 81 breeding territories considered in this study: 0.73 m, range: 0.16–2.95 m).

Catching, marking, individual identification, and survival estimates

Prior to observations, in September and early October 2012, all but one of the 37 focal males and 78 of the respective 81 dominant females were caught using hand-nets and Plexiglass tubes (Balshine-Earn et al. 1998). We recorded the SL of all fish to the nearest mm (average size of males: 6.1 cm, range: 5.5–6.5 cm; average size of females: 5.2 cm, range: 4.6–5.9 cm), took a small fin clip for genetic fingerprinting (see below), and individually marked each fish with visible implant elastomers (Northwest Marine Technology, Shaw Island, WA). In September 2013, we recaptured all individual fish bearing marks, recorded their current home territory, their current social status, measured their SL, and again took a small fin clip. In addition, we caught 27 large individuals not bearing any visible marks, but potentially having been focal fish of this study in 2012. The elastomer marks allowed us to reliably identify individuals during the observation period in 2012, but by 2013, some marks had faded or completely disappeared. We thus exclusively relied on genetic methods for the identification of individuals between years

and only considered fin clips to belong to the same individual that had a 100% match for all 13 microsatellites (see below).

We consider any fish caught and marked in 2012 and not recaptured in 2013 as having died between 2012 and 2013 for the following reasons: 1) We thoroughly checked all dominant individuals found in the focal colony in 2013 for any hint of previous marking and also caught fish for which we were in doubt. 2) Of the 27 large individuals caught in 2013 that did not bear marks, only a single one proved to have been a focal fish of this study in 2012 that had lost its marks completely. This makes it unlikely that we missed many fish that had lost their marks or went undetected. 3) Long distance dispersal is rare in this species (Stiver et al. 2004) and we also worked in other colonies within the same population in 2013 where we checked for marked fish. This makes it unlikely that a large proportion of fish dispersed beyond our detection range.

Focal observations

Between 11 October 2012 and 18 November 2012, we carried out 9–12 observations of each focal male. Each focal observation lasted 7 min, during which a male's position and behavior were continuously recorded. A male's position was determined as either outside or inside one of its breeding territories, and for each recorded behavior, we noted where it was carried out (i.e., outside territories or within a specific breeding territory). The recorded behaviors included 1) all overt and restrained aggressive behaviors (Balzarini et al. 2014) directed toward 1a) heterospecifics that posed a threat to the male (mainly large *Lepidolamprologus elongatus* and mastacembelid eels), 1b) heterospecifics that were no threat to the male but which potentially posed a threat to juveniles and subordinate *N. pulcher* (see Heg et al. 2008), 1c) dominant females from own breeding groups, and 1d) large foreign conspecifics (i.e. fish not belonging to the focal's groups); 2) territory maintenance (i.e., digging out shelters and removal of snails and debris); and 3) feeding bites (i.e., single bites in an attempt to feed on plankton either in the water column or on substrate). Throughout this paper, counts of behaviors are given per 7 min, if not specified otherwise. Furthermore, we calculated for each male the time he spent in breeding territories (as proportion of total observation time), and for each breeding territory, the time the respective male spent in it (also as proportion of total observation time).

Measures of paternal care

We considered a male's aggression against heterospecifics that did not pose a direct threat to himself as a form of paternal care because such fish may prey on eggs, larvae, fry, and/or juveniles, depending on their size (Heg et al. 2008). Maintenance behaviors such as digging and removing debris were also considered a form of paternal care, because in this population, *N. pulcher* breed in shelters dug out under stones (Balshine et al. 2001). Larvae and free-swimming fry subsequently use such breeding shelters for protection (Taborsky 1984). Sand in shelters has been shown to be a source of mortality for young offspring in this species (Taborsky and Limberger 1981). Furthermore, a male's presence in a territory may relate also to other (unrecorded) forms of care (e.g., vigilance or predator deterrence through the male's presence), and we consequently considered time spent in a breeding territory also as a measure of paternal care.

Potential costs to males

To unravel whether increased paternal care or defending the dominant position in more groups is costly to males, we measured male

time budgets, their feeding behavior, and the amount of aggressive interactions they had with foreign conspecifics. Large individuals of *N. pulcher* perform most of their feeding activity outside of their territories in the water column (Gashagaza 1988). Thus, spending time in territories and performing care may reduce their food intake, especially for males that defend several territories (Desjardins, Fitzpatrick, et al. 2008). Males also appear to face increased intrasexual conflict, as indicated by shorter tenure times and lower survival of males compared with females (Dierkes et al. 2005), and an operational sex ratio biased toward females (Desjardins, Fitzpatrick, et al. 2008). Subordinate males also rarely inherit the dominant position in their group, which is typically taken over by foreign individuals (Stiver et al. 2006). Importantly, breeder males are much larger than breeder females (Balshine et al. 2001), and we only scored aggressive interactions between focal males and similar-sized individuals as cases of “aggression toward large foreign conspecifics.” Thus, aggressive interactions between dominant males and large foreign conspecifics may constitute a form of competition over territory ownership, and may prove costly if they reduce male survival and/or tenure.

Potential costs to females

One of the ultimate reasons for sociality in *N. pulcher* appears to be antipredator defense provided by large individuals, which increases the survival of juveniles and smaller subordinates (Taborsky 1984; Heg et al. 2004). Dominant males provide a considerable share of such antipredator defense (Desjardins, Stiver, et al. 2008; Heg and Taborsky 2010). Thus, if males have to divide their time and effort between several breeding groups, this may be costly to individual females because their respective group is less well defended. It has been shown that females paired with polygynous males do not compensate for the reduced male effort they receive, and no other costs to females could yet be detected (Desjardins, Fitzpatrick, et al. 2008; Wong et al. 2012). However, such costs might accrue over longer time periods, manifested in reduced female survival and/or tenure. Finally, males may behave aggressively toward females and it has been suggested that the costs of such aggression may be higher for females paired with more competitive males (Wong et al. 2012).

Genetic methods

The following 13 microsatellite loci were used to identify individuals caught in 2012 and 2013, based on the DNA extracted from the respective fin clips: NP007, NP773, UL12 (Schliewen et al. 2001); Pzeb4 (Van Oppen et al. 1997); TmoM11, TmoM13, TmoM25, TmoM27 (Zardoya et al. 1996); UME003 (Parker and Kornfield 1996); UNH106, UNH154 (Lee and Kocher 1996); UNH1009 (Carleton et al. 2002); Ppun21 (Taylor et al. 2001). All loci had 2–27 alleles, with a mean of 14 alleles per locus. Identity checks were performed with the Microsatellite Toolkit, an add-in of Microsoft Excel. DNA extraction and amplification followed the protocol described by Bruinjes et al. (2011).

Statistical analyses

All statistical analyses were carried out using R version 3.1.2 (R Development Core Team 2013). Generalized linear mixed effects models (GLMM) were fitted using the R package lme4 version 1.1–7 (Bates et al. 2013). 1) To test whether our proposed measures of paternal effort were correlated, we fitted GLMMs with logarithmic link function (GLMM log link; family: Poisson) to account for

the assumed Poisson structure of the data. A total of 3 such models were fitted in order to correlate each of the paternal care measurements with the other two. These models included 1 response variable (“aggression toward medium/small heterospecifics” or “maintenance behaviors”), 1 explanatory variable (“time in territory” or “maintenance behaviors”), and a male’s identity as random factor. 2) To test whether males defending different numbers of territories differed behaviorally, we fitted generalized linear models with logarithmic link function (GLM log link; family: quasi-Poisson) to account for the assumed Poisson structure of the data. These models included 1 response variable each (“aggression toward heterospecifics that do not pose a threat to the male,” “maintenance behaviors,” “time in territories,” “aggression toward dominant females of own breeding groups,” “aggression toward large foreign conspecifics,” “feeding bites,” or “aggression toward heterospecifics that pose a threat to the male”) and 1 explanatory variable each (“number of territories defended in 2012”). 3) To test whether females received different amounts of paternal effort and/or male aggression, we fitted GLMMs log link. These models included 1 response variable each (“dominant male’s aggression toward heterospecifics that do not pose a threat to the male performed in the female’s breeding territory,” “dominant male’s maintenance behaviors performed in the female’s breeding territory,” “proportion of total observation time the dominant male spent in the female’s breeding territory,” “aggressions the female received from the dominant male,” or “dominant male’s aggression toward heterospecifics that pose a threat to the male performed in the female’s breeding territory”), 1 explanatory variable each (“number of territories defended by the respective male in 2012”), and a male’s identity as random factor. 4) To test whether productivity was influenced by the number of territories a male defended, we fitted a GLM log link and a GLMM log link. These models included 1 response variable each (GLM: “number of juveniles found in all of the male’s breeding territories”; GLMM: “juveniles found in the female’s territory”), 1 explanatory variable (“number of territories defended by the respective male in 2012”). The GLMM also included a male’s identity as random factor. 5) To test whether male survival differed between males that defended different numbers of territories, were of different size, defended groups of different size, and/or that differed behaviorally, we fitted a GLM with logistic link function (GLM logit link; family: binomial) to account for the binomial structure of the data. This model included a single response variable (“male survival to 2013: yes/no”) and 9 explanatory variables (“number of territories defended in 2012,” “male SL,” “average group size,” “time spent in breeding territories,” “aggressions toward heterospecifics that pose a threat to the male,” “aggressions toward heterospecifics that do not pose a threat to the male,” “aggression toward large foreign conspecifics,” “feeding bites,” and “maintenance behaviors”). 6) To test whether female survival differed between females that were mated to males that defended different numbers of territories in 2012, were of different size, belonged to groups of different size, and/or received different amounts of paternal effort or male aggression, we fitted a GLMM with logistic link function (GLMM logit link; family: binomial) to account for the binomial structure of the data. This model included a single response variable (“female survival to 2013: yes/no”) and 8 explanatory variables (“total number of breeding territories the male defended in 2012,” “female SL,” “group size,” “dominant male’s aggression toward heterospecifics that do not pose a threat to the male performed in the female’s breeding territory,” “dominant male’s maintenance behaviors performed in the female’s breeding territory,” “proportion of total observation

time the dominant male spent in the female's breeding territory," "aggressions the female received from the dominant male," "dominant male's aggression toward heterospecifics that pose a threat to the male performed in the female's breeding territory"). We also included male identity as random factor. 7) To test whether females that survived to 2013 were more or less likely to still be paired with the same male as in 2012 depending on the number of breeding territories their mate defended in 2012, we fitted a GLMM logit link. This model included 1 response variable ("same mate in 2012 and 2013: yes/no"), 1 explanatory variable ("total number of breeding territories the male defended"), and a male's identity as random factor. 8) To test whether groups were more or less likely to retain the same breeders between years depending on the number of breeding territories the respective male defended in 2012, we fitted 2 GLMMs logit link. These models included one of 2 response variables each ("identical breeding pair in 2012 and 2013: yes/no" or "at least one breeder identical in 2012 and 2013: yes/no"), 1 explanatory variable ("total number of breeding territories the male defended"), and a male's identity as random factor.

RESULTS

Correlations between paternal care behaviors

All 3 measures of paternal care effort (i.e., aggression against heterospecifics that did not pose a direct threat to the male, territory maintenance behaviors, and time spent in a breeding territory) were highly correlated with each other: Males attacked small- to medium-sized heterospecifics more often in territories in which they spent more time (GLMM: $n = 81$, $\zeta = 77.35$, $P < 0.001$) and where they showed more maintenance behaviors (GLMM: $n = 81$, $\zeta = 55.75$, $P < 0.001$), and males also performed more maintenance in territories in which they spent more time (GLMM: $n = 81$, $\zeta = 64.36$, $P < 0.001$).

Effects of polygyny on male behavior

Males that defended more territories had more aggressive encounters with large foreign conspecifics (GLM: $n = 37$, $t = 2.64$, $P = 0.012$; Figure 1) and showed more aggression against heterospecifics that posed a threat to the male (GLM: $n = 37$, $t = 2.59$, $P = 0.014$). However, males spent similar proportions of total observation time in all of their breeding territories, irrespective of the number of territories they defended (GLM: $n = 37$, $t = 0.575$, $P = 0.57$; Figure 2a). There was also no correlation between the number of territories defended and 1) a male's total aggression toward predators that did not pose a threat to himself (GLM: $n = 37$, $t = 0.02$, $P = 0.98$), 2) the total number of maintenance behaviors performed by a male (GLM: $n = 37$, $t = -1.46$, $P = 0.15$), 3) the total amount of aggression a male showed toward his mates (GLM: $n = 37$, $t = -0.22$, $P = 0.83$), and 4) the number of feeding behaviors a male showed (GLM: $n = 37$, $t = -0.19$, $P = 0.85$).

Effects of polygyny on females

Females paired with males that defended more territories received reduced paternal effort: The more other breeding territories a female's mate defended, 1) the less time he spent in a given female's breeding territory (GLMM: $n = 81$, $\zeta = -13.45$, $P < 0.001$; Figure 2b), 2) the less maintenance he performed in a given female's breeding territory (GLMM: $n = 81$, $\zeta = -1.96$, $P = 0.05$), and 3) the less aggression he showed toward heterospecifics that did

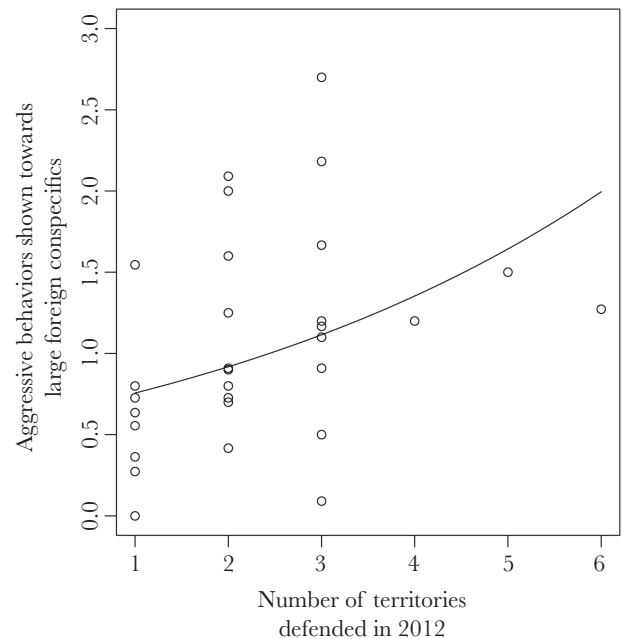


Figure 1

The number of aggressive behaviors a focal dominant male showed toward large foreign conspecifics during 7 min of observation time as a function of the number of breeding territories in which the male defended the dominant breeder position. Each circle represents an individual focal male and indicates the mean aggression recorded during 9–12 observations. The trend line is based on the respective GLM and depicts a significant relationship (cf., Methods and Results).

not pose a threat to himself in a given female's territory (GLMM: $n = 81$, $\zeta = -3.88$, $P < 0.001$). However, females received similar amounts of aggression from their mate, irrespective of how many territories he defended (GLMM: $n = 81$, $\zeta = -0.14$, $P = 0.89$). Also, male aggression toward heterospecifics that posed a threat to himself were similar in female breeding territories, irrespective of the number of territories a male defended (GLMM: $n = 81$, $\zeta = -0.31$, $P = 0.75$).

Effects of polygyny on reproduction

The more breeding territories a male defended, the more juveniles were produced in his territories (i.e., in all of his breeding territories combined; GLM: $n = 37$, $t = 7.07$, $P < 0.001$). There was no effect of the number of breeding territories a female's mate defended on the number of juveniles in the respective female's territory (GLMM: $n = 81$, $\zeta = 1.57$, $P = 0.12$).

Effects of polygyny on survival, pair stability, and group tenure

Of the 36 dominant males caught and marked in 2012, 17 were recaptured in 2013. Males that had spent more time in breeding territories in 2012 were more likely to survive to 2013 (Figure 3; Table 1), and there was a trend for males, which defended less against heterospecifics that did not pose a threat to themselves, to survive better (Table 1). No other factor we considered influenced male survival between 2012 and 2013 (Table 1). Of the 78 females caught and marked in 2012, 59 were recaptured in 2013. Female survival was not significantly influenced by any of the factors we considered (Table 2). For 57 of the females that survived to 2013, we also knew the identity of their mate in 2012.

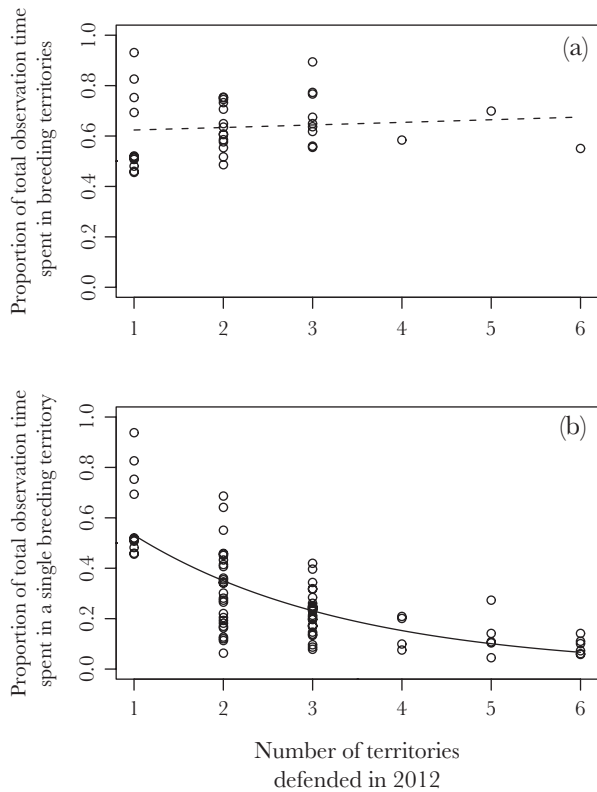


Figure 2

Proportions of total observation time males spent in breeding territories in which they defended the dominant breeder position. (a) Proportion of total observation time males spent in any of their respective breeding territories as a function of the number of territories in which they were dominant. (b) Proportion of total observation time males spent in a particular breeding territory as a function of the total number of territories in which they were dominant. In (a) each circle represents an individual focal male and indicates the proportion of time he spent in breeding territories during 9–12 observations. In (b) each circle represents a single breeding territory and indicates the proportion of time the respective dominant male spent in it during 9–12 observations. The trend lines are based on the respective GLM and GLMM and depict a nonsignificant relationship in (a) and a significant relationship in (b) (cf., Methods and Results).

Of these, 15 were mated with the same male in both years, and this was not influenced by the number of breeding territories the male defended in 2012 (GLMM: $n = 57$, $\chi^2 = -532$, $P = 0.47$). We knew the identity of the breeder male in 2012 for 79 groups, the identity of the breeder female in 2012 for 78 groups, and had full information about the breeder pair in 2012 for 76 groups. A total of 58 groups retained at least one of their breeders from 2012 to 2013, and the probability of retaining a breeder was not influenced by the number of territories the respective dominant male defended in 2012 (GLMM: $n = 78$, $\chi^2 = 1.16$, $P = 0.25$). Similarly, a total of 14 groups retained the same breeder pair between 2012 and 2013, and the probability of doing so was also not influenced by the number of territories the male defended in 2012 (GLMM: $n = 76$, $\chi^2 = -0.85$, $P = 0.37$). The discrepancy between the number of females retaining the same mate between 2012 and 2013 ($n = 15$) and the number of groups retaining the same breeder pair between 2012 and 2013 ($n = 14$) was caused by a single female that dispersed between years to a different territory defended by the same male.

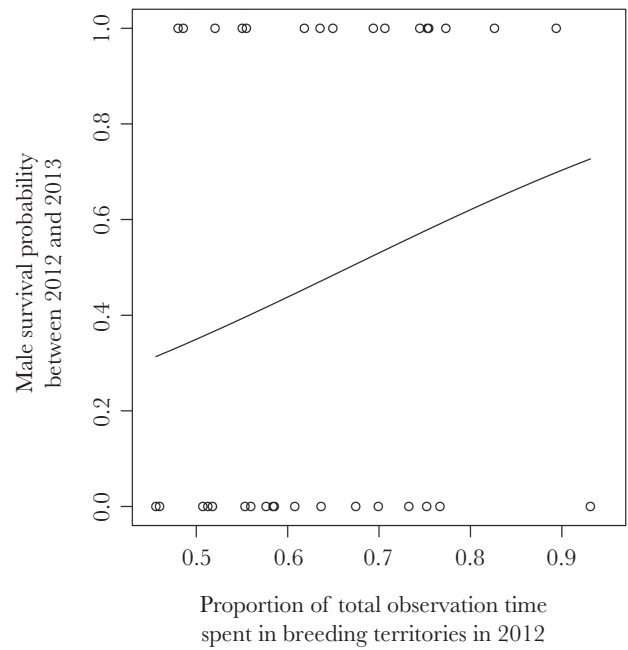


Figure 3

A male’s probability to survive between 2012 and 2013 as a function of the proportion of total observation time he spent in breeding territories. Each circle represents an individual focal male and gives the proportion of time he spent in breeding territories during 9–12 observations. The trend line is based on the respective GLM and depicts a significant relationship (cf., Methods and Results).

Table 1

Analysis of factors influencing male survival

	Estimate	Standard error	χ^2 value	P value
Number of territories defended	-0.18	0.46	-0.38	0.7
Male size	-0.54	1.96	-0.27	0.78
Group size	0.39	0.32	1.22	0.21
Time in territories	8.76	4.53	1.93	0.035
Aggression toward large heterospecifics	2.13	3.15	0.68	0.49
Aggression toward small/medium heterospecifics	-0.71	0.45	-1.57	<i>0.086</i>
Aggression toward large foreign conspecifics	0.29	0.85	0.34	0.73
Feeding bites	0.06	0.04	1.38	0.12
Maintenance behaviors	0.24	0.38	0.63	0.54

A GLM logit link was fitted to unravel factors influencing the survival of focal males between 2012 and 2013 ($n = 36$). The considered factors (all recorded in 2012) were as follows: the number of breeding territories in which a male defended the dominant breeder position (“number of territories defended”), a male’s SL (“male size”), a male’s groups’ size (averaged for polygynous males; “group size”), the proportion of total observation time a male spent in breeding territories (“time in territories”), the number of aggressive behaviors a male directed toward heterospecifics that posed a threat to himself (“aggression toward large heterospecifics”), the number of aggressive behaviors a male directed toward heterospecifics that did not pose a threat to himself (“aggression toward medium/small heterospecifics”), the number of aggressive encounters a male had with large foreign conspecifics (“aggression toward large foreign conspecifics”), the number of feeding behaviors the male performed (“feeding bites”), and the number of maintenance behaviors the male performed (“maintenance behaviors”). Significant relationships are printed in bold face, and nonsignificant trends are italicized.

Table 2
Analysis of factors influencing female survival

	Estimate	Standard error	ζ value	<i>P</i> value
Number of territories defended	-0.18	0.35	-0.51	0.57
Female size	1.85	1.71	1.08	0.16
Group size	-0.11	0.14	-0.76	0.45
Time in territory	-0.45	3.53	-1.23	0.9
Aggression received	1.41	5.01	0.28	0.78
Aggression toward large heterospecifics	0.08	3.1	0.03	0.98
Aggression toward small/medium heterospecifics	-0.14	0.42	-0.33	0.75
Maintenance behaviors	-0.3	0.31	-0.98	0.32

A GLMM logit link was fitted to unravel factors influencing the survival of females mated with focal males between 2012 and 2013 ($n = 78$). The considered factors (all recorded in 2012) were as follows: the total number of breeding territories in which a female's mate defended the dominant breeder position ("number of territories defended"), a female's SL ("female size"), a female's group's size ("group size"), the proportion of total observation time a female's mate spent in her territory ("time in territory"), the number of aggressive behaviors a female received from her mate ("aggression received"), the number of aggressive behaviors a female's mate directed toward heterospecifics that posed a threat to himself in the female's territory ("aggression toward large heterospecifics"), the number of aggressive behaviors a female's mate directed toward heterospecifics that did not pose a threat to himself in the female's territory ("aggression toward small/medium heterospecifics"), and the number of maintenance behaviors a female's mate performed in her territory ("maintenance behaviors").

DISCUSSION

In *N. pulcher*, males defending more breeding territories have more aggressive interactions with potential rivals (Figure 1), and they attack potentially dangerous heterospecifics more often. These apparent costs do, however, not translate into reduced survival. This may be explained by the fact that polygyny does not affect a male's paternal care effort (Figure 2a) or feeding behavior. Rather, males that spent more time in breeding territories enjoyed increased survival, irrespective of the total number of breeding territories they defended (Figure 3). Polygyny does thus appear to be favorable for males because they enjoy greater reproductive output the more territories they defend, at no apparent cost. Females mated with males that defended more other breeding territories received less paternal care for their own breeding group (Figure 2b; see also Desjardins, Fitzpatrick, et al. 2008), but this did not result in lowered female survival. Female productivity was also not reduced by polygyny, and females received similar amounts of male aggression, irrespective of the male's harem's size. Thus, our data suggest that polygyny is not costly to females. As a consequence of the similar survival rates, pair stability and breeder tenure did not systematically change with the number of territories a respective male defended.

The lack of any detectable fitness costs of polygyny for either males or females in our study is remarkable. In birds, reduced paternal effort usually leads to reduced reproductive success for females paired with polygynous males (Webster 1991). As a consequence, males and females in such species have conflicting interests concerning the mating system (Chapman et al. 2003). For *N. pulcher*, however, no such differences in offspring survival were detected (Desjardins, Fitzpatrick, et al. 2008), but it was hitherto unclear whether costs of polygyny might accrue over longer periods of time, via reduced breeder survival under polygynous conditions. No such differential survival was detected in our study, which refutes

this hypothesis. Although a long-term study on pied flycatchers also found no negative impact of polygyny on female survival, female reproductive success is indeed reduced in this species when the respective male is polygynous (Huk and Winkel 2006). Thus, contrary to the situation in birds, there appears to be no conflict of interest between the sexes over the mating system in *N. pulcher*, as had been suggested previously (Desjardins, Fitzpatrick, et al. 2008; Wong et al. 2012).

We had initially interpreted increased time spent in breeding territories as costly to males because it reduces the time they can spend feeding in the water column (Gashagaza 1988), potentially hampering their survival (Santos and Nakagawa 2012). Contrary to our expectation, males that spent more time in breeding territories showed increased survival (Figure 3). Thus, although time spent in a territory may be used as a proxy of paternal care effort because it was highly correlated with our other measures of paternal care, it is apparently not traded-off against survival. Males that spend more time in breeding territories may still incur costs, for example, via reduced chances of attaining additional breeding territories (Magrath and Komdeur 2003), but such claims are beyond the scope of this study and future work in that direction is needed.

Increased intrasexual conflict among males is a proposed cost of polygyny (Shuster and Wade 2003). We find that males that defended more territories indeed engaged in aggressive interactions with potential rivals more often (Figure 1). However, as this did not result in lowered survival or shorter tenure, it may not constitute an actual cost, but rather a by-product of the enlarged male territory.

Finally, we had expected groups defended by polygynous males to experience reduced breeder tenure, either through reduced male or female survival. Such shorter tenure might prove costly because it may perturb a group's stability (Wong and Balshine 2011) and it may reduce relatedness within groups (Dierkes et al. 2005). However, we find no evidence for an influence of polygyny on tenure of either males or females. Although male survival was generally lower than female survival (47% and 76%, respectively), neither did consistently vary with the number of territories a male defended. Breeder turnover was generally high, with only 18% of breeding groups (14 out of 76) retaining the same breeder pair between 2012 and 2013, whereas 74% of groups (58 out of 78) retained one of their breeders. Consequently, roughly one-fifth of offspring produced in 2012 would have helped to raise their full-siblings in 2013, whereas three-quarters of offspring would have helped to raise half-sibs. These findings are in line with earlier work on within-group relatedness in *N. pulcher*, which proposed matrilineal and generally low within-group relatedness in this species (Dierkes et al. 2005). Although within-group relatedness appears to be even lower in polygynous groups (Wong et al. 2012), we cannot show that this is an effect of shorter breeder tenure due to polygyny.

It is important to note that our resolution is very low concerning survival probabilities. All focal fish survived throughout our observation period in 2012, but it is unclear at which point of the interval before recapture in 2013 those fish that were not found again actually died. In addition, we do not know for how long our focal individuals had been breeders in their respective territory previous to our observations in 2012. Thus, there may still be costs of polygyny expressed in reduced tenure or survival that remained undetected by our study. Furthermore, our measure of reproductive output, that is, counts of juvenile fish below helper size, is an approximation that may suffer from several uncertainties: The parentage of the respective juveniles was not determined because we did not collect any small fish in order to not

disturb or destroy groups. Hence, a proportion of the counted juveniles were probably not the offspring of our focal breeders, but rather offspring of other individuals (either helpers or members of other groups; cf., Dierkes et al. 2008; Hellmann et al. 2015). Thus, costs of polygyny might accrue through reduced reproductive output, either due to shortened tenure or reduced paternity/maternity. Future studies should monitor individual survival over even longer time periods and try to assess actual reproductive success of individuals in order to resolve the apparently paradoxical findings of our study, where costs of polygyny are detected at the behavioral level but do not translate into different approximations of fitness between monogamous and polygynous breeding conditions. There is likely less variance and more precision in the estimates of parental care than in the fitness proxies we could use in this study.

In summary, our results suggest that in *N. pulcher* polygyny does not constitute a conflict of interest between males and females, as it does increase male reproductive success at no apparent cost to either the respective male or its mates (see also Desjardins, Fitzpatrick, et al. 2008; Wong et al. 2012). However, the potential for polygynous mating and the benefits males derive from it appear to affect the species' ecology in several ways: Although the sexes are generally monomorphic, 1) male breeders are larger than female breeders (Balshine et al. 2001; this study). Small size differences reliably predict the winner of a conflict in *N. pulcher* (Reddon et al. 2011), thus larger size in males may be a result of increased intrasexual conflict over breeding positions. This is further supported by the finding that 2) male breeders have lower survival than female breeders (Dierkes et al. 2005; this study). A consequence of this reduced male survival is lower relatedness between subordinate group members and the respective dominant breeder male compared with their relatedness to the breeder female (Dierkes et al. 2005). This finding is further corroborated by the fact that 3) male breeder vacancies are typically taken over by foreign fish joining a group, whereas female subordinates more frequently inherit the breeding position in their group (Stiver et al. 2006). This may also explain why 4) dispersal appears to be male biased in this species (Stiver et al. 2004, 2007). Thus, polygyny constitutes an important factor in *N. pulcher*'s ecology, albeit not by increasing sexual conflict, but by favoring different life-history trajectories in males and females.

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