



## Costs and benefits of polygyny in the cichlid *Neolamprologus pulcher*

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Polygyny is regarded as a beneficial strategy for males, whereas females mated with polygynous males (males simultaneously paired to more than one female) often suffer a reduction in pair male contributions. This study examined the costs and benefits associated with polygyny in the cooperatively breeding cichlid *Neolamprologus pulcher*. In this species, males are facultatively polygynous; some males hold only one territory with one breeding female whereas other males hold multiple territories, each with its own breeding female. Polygynous males were larger than monogamous males and body-scraped less, a behaviour often associated with ectoparasite loads. Polygynous males also had larger testes (controlling for body mass) and higher circulating 11-ketotestosterone levels than monogamous males. Paradoxically, monogamous males occupied higher-quality territories with more shelter and fewer predators. Monogamous males also provided more parental care than polygynous males but the number and survival of young did not vary according to male mating behaviour. The results of our study suggest that females trade-off between male genetic quality and resources in *N. pulcher*. Our results imply that males holding only one territory may provide their mates with significant assets but may not be able to outcompete neighbours for additional breeding positions because of their small body size and possible higher parasite load. The lack of differences between monogamous and polygynous groups in terms of offspring survival (a measure of reproductive success) suggests that there may be few if any fitness consequences of polygynous pairing for females.

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The evolution of polygyny typically is easily explained from the males' perspective because males increase their reproductive success by gaining access to many fertile females (Orians 1969; Trivers 1972; Emlen & Oring 1977; Hasselquist 1998). It is more difficult to explain why females mate with polygynous (already mated) males because these females often suffer costs from such matings

(Verner & Willson 1966; Westneat 1988; Slagsvold & Lifjeld 1994; Pribil & Searcy 2001). In species where care is important for the survival of the young, females in polygynous groups regularly receive less male assistance and often have lower reproductive success than females paired with monogamous males (Slagsvold & Lifjeld 1994; Eens & Pinxten 1995; Kempenaers 1995; Czapka & Johnson 2000). Consequently, it is difficult to explain theoretically why females would mate with polygynous males. In the real world, mating behaviour is not often the choice of only one sex but instead is more likely the outcome of a conflict between the sexes (Davies 1989). Explaining the evolution and maintenance of polygyny in light of sexual conflict is an area of current active research (Rowe et al. 1994; Chapman et al. 2002; Houston et al. 2005; Parker 2006). In this study, we set out to explore correlates

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of polygyny and to identify possible sources of sexual conflict in a cichlid fish.

Several factors have been suggested to select for polygyny (Emlen & Oring 1977; Searcy & Yasukawa 1989). Female-biased sex ratios, in which females have few alternative breeding options, have been shown to lead to polygyny (Smith et al. 1982; Kempenaers 1994; Pinxten & Eens 1997). However, Trivers (1972) argued that a female-biased sex ratio is derived from the mating system and is not a causal factor. Polygyny is also expected to arise when resources and/or females are spatially clustered; when territories can support multiple females, females can be easily monopolized by a single male (Emlen & Oring 1977). Females also may benefit more from mating with an already mated male if this ensures them access to a high-quality mate or a high-quality territory with many resources (Verner 1964; Verner & Willson 1966; Orians 1969). In these situations females will often experience a trade-off between the quality of their mate or territory and the amount of paternal care that would be provided (Dyrce 1986; Webster 1991a, b; Kempenaers 1994; Slagsvold & Lifjeld 1994).

Degrees of sexual dimorphism in body size and reproductive investment often differ between monogamous and polygynous species. Polygynous species are associated with more extreme sexual size dimorphism and greater male gonadal investment than what is found in closely related monogamous species (Luetenegger 1978; Gage 1994; Fairbairn 1997; Balshine et al. 2001). Also, steroid hormone fluctuations vary with mating systems (Oliveira et al. 2001). Polygynous species, where males provide little to no paternal care and compete to attract females throughout the breeding season, have been shown to maintain high levels of plasma androgens (at or near their physiological maximum) (Wingfield et al. 1990). In contrast, socially monogamous males that provide paternal care maintain low androgen levels (near the breeding baseline) and show dramatic increases in androgens only in the event of sporadic male–male competition (Wingfield et al. 1990). This idea is known as the challenge hypothesis and has received support in many studies of birds (e.g. Ferree et al. 2004; Geslin et al. 2004; Smith et al. 2005) mammals (e.g. Goymann et al. 2003; Muller & Wrangham 2004) and fish (e.g. Hirschenhauser et al. 2004; Desjardins et al. 2006). However, to date, no study has examined how androgen levels, specifically testosterone (T) and 11-ketotestosterone (11KT; a primary androgen in fish), differ between males and females in species in which males adopt different mating strategies.

In this study we used the mixed mating system found in the cooperatively breeding cichlid fish *Neolamprologus pulcher* to explore the behavioural and physiological correlates of multiple versus single pair bonds in males. *Neolamprologus pulcher* is particularly well suited to this investigation since males are either socially monogamous (occupying a single territory containing a breeding female and a series of helpers) or socially polygynous (holding the dominant breeding position in multiple territories, each containing its own breeding female and helpers) (Limberger 1983), and females may choose males based on these territory characteristics. The aims of our study

were (1) to investigate the morphological, physiological and behavioural correlates of males and females adopting these two mating options, (2) to characterize the differences in group composition and territory quality between monogamous and polygynous groups and (3) to explore the costs and benefits for females associated with monogamy versus polygyny in an attempt to explain the mixed mating strategy in *N. pulcher*.

## METHODS

### Study Species, Field Site and Behavioural Measures

*Neolamprologus pulcher* lives in social groups consisting of a dominant breeding pair and 1–20 other male and female individuals ('helpers') that assist in all aspects of care (Taborsky & Limberger 1981; Taborsky 1984, 1985; Balshine-Earn et al. 1998; Stiver et al. 2005; Heg et al. 2005). Parental care by breeders and allocare by helpers consist of territory/nest defence, territory/nest maintenance and direct brood care (fanning and cleaning of the eggs and larvae). Such allocare has been shown to enhance the frequency of breeding events, the number of young produced and offspring survival within the group (Taborsky 1984; Balshine et al. 2001; Brouwer et al. 2005). When not providing care, individual *N. pulcher* feed on zooplankton (usually in the water column) and engage in aggressive and nonaggressive social contact with other members of their group and with conspecifics from other groups in their subpopulations.

Our study area in Kasakalawe Bay, Lake Tanganyika (Zambia: 8.5°S, 31.05°E) consists of thousands of groups of fish divided into nine subpopulations. Between 2 February and 28 April 2005 we collected group composition and mating/pairing data from a sample of 254 *N. pulcher* groups from all nine subpopulations (see Balshine et al. 2001; Stiver et al. 2007). Groups were found at depths of 8.5–12 m and were observed using SCUBA. Each group's territory was marked with a uniquely labelled rock and group size, and composition was determined in two or three 5-min observational visits. Of the groups observed in our study area, we targeted 59 groups for close behavioural monitoring and sampling. Thirty-eight of the targeted groups were polygynous (a breeding female and her helpers and the polygynous male associated with this group) and 21 were monogamous groups (a breeding pair and their helpers). The numbers of monogamous and polygynous groups studied did not reflect the proportion of monogamous and polygynous groups in the study area (see Results) and did not represent a random sample of the groups in the study area. Polygynous males were males that participated in parental care in multiple groups and polygynous females were female breeders that were assisted in parental care by a polygynous male. A polygynous group refers to one of a polygynous male's territories consisting of one female and her associated helpers. Each individual in each of the 59 groups was reliably identified using a combination of underwater size estimates and specific individual markings including fin clipping and

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