

Carsten Schradin · Jürg Lamprecht

Female-biased immigration and male peace-keeping in groups of the shell-dwelling cichlid fish *Neolamprologus multifasciatus*

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Abstract The small cichlid fish *Neolamprologus multifasciatus* is endemic to Lake Tanganyika and is unique among fish because it lives in complex social groups with several reproductive males and females, all of which participate in defending their territory against neighbors and intruders. Individuals use empty snail shells for breeding and shelter. Previous parentage analysis using microsatellites suggested occasional exchange of individuals between groups. In field experiments, we found that females showed a higher tendency than males to migrate into territories already occupied by a resident pair. The phenomenon and causes of female-biased immigration were further investigated in aquarium experiments: Nine of 15 females, but only 2 of 15 equally sized males, settled in territories of established pairs. Territorial males exhibited more aggression toward strange males (potential reproductive competitors) than toward strange females (potential additional mates); their females were more aggressive toward strange females (probably competitors for shells) than toward strange males. Apparently, a conflict exists between the sexes regarding the immigration of additional females. This conflict seems to be the selective basis for observed active male interference in aggressive disputes between females in the territory. Interfemale tolerance in a group was greater in the male's presence than in his absence.

Key words Female-biased immigration · Sexual conflict · Male peace-keeping · *Neolamprologus multifasciatus*

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C. Schradin (✉) · J. Lamprecht
Max-Planck-Institut für Verhaltensphysiologie, Seewiesen,
Postfach 1564, 82305 Starnberg, Germany

Present address:

C. Schradin, Anthropologisches Institut und Museum,
Universität Zürich, Winterthurerstrasse 190,
8057 Zürich, Switzerland,
e-mail: schradin@aim.unizh.ch
Tel.: +41-1-6355446, Fax: +41-1-6356804

Introduction

Complex social systems were initially described and studied mainly in birds and mammals. However, the great variety of reproductive strategies and social systems more recently found in fishes (e.g., Taborsky 1994; Wisenden 1999) can offer special opportunities for studying complex social phenomena because small home ranges and ease of rearing many species in the laboratory make them readily amenable to experimental manipulation. Examples of interesting social behaviors studied include bigamy and mate desertion (Keenleyside 1983, 1985; Triefenbach and Itzkowitz 1998), helping behavior (Taborsky 1985), adoption (Wisenden and Keenleyside 1994), and mate choice copying (Dugatkin and Godin 1992; Schlupp and Ryan 1997).

The evolution of mating systems is often strongly influenced by food distribution (e.g., Wrangham 1980; Davies and Lundberg 1984) and predation risk (e.g., van Schaik 1983; Magurran and Seghers 1994). They largely determine the degree of gregariousness. More details are usually added to a social system by two types of conflict: (1) between conspecifics over access to mates, which depends on the operational sex ratio, and can differ largely between the sexes (Trivers 1972; Emlen and Oring 1977; Reynolds 1996), and (2) between the sexes (Davies 1989; Andersson 1994; Magurran and Seghers 1994; Clutton-Brock and Parker 1995; Henson and Warner 1997). These may lead to coercion and other ways of limiting the partner's options. Resultant social systems can be very diverse and variable (e.g., Lott 1991).

We studied sex differences of *Neolamprologus multifasciatus* with regard to immigration into territories of established pairs, and the resident males' and females' behavior towards male and female intruders, to search for intra- and intersexual conflicts, which are likely to have shaped the complex social system of this fish. *N. multifasciatus* is endemic to Lake Tanganyika (Africa), and is probably the smallest cichlid fish. Males grow up to 3 cm in length, females to just over 2 cm in the wild,

where the species lives in complex social groups (Kohler 1997), which conform to what Emlen (1995, 1997) has defined as “extended families”: they are “families” in the sense that offspring remain in contact with their parents beyond sexual maturity and are called “extended” because “two or more relatives of the same sex reproduce” within the group (Emlen 1995, p. 8,093). This fish lives in groups with several reproductive males (one to three) and females (one to five) and their offspring, often from several clutches. Group members tend to join in defense of their territory against neighboring groups and intruders.

N. multifasciatus occurs most commonly on so-called shell-beds (Cohen 1989), i.e., accumulations of empty shells of the endemic water snail *Neothauma*, often spread over many square kilometers. They use empty snail shells for breeding and shelter (see also Büscher 1986; Staeck and Staeck 1991). Where the shells are covered with a layer of sand, as is the case in many areas, they must be dug up before use, i.e., the fish carry mouthfuls of sand from the shells in the center to the territorial boundary. A group territory consists of a depression or pit in the sand, containing a number of excavated, intact shells, generally exceeding the number of adult individuals in the group. Group territories are situated next to each other, forming large colonies. Individuals feed on plankton in the water column above the territory (Kohler 1997).

Intact and unoccupied shells are a scarce resource for two reasons: (1) shells that are already dug up are always inside a territory, which is defended by the group against intruders, and (2) encounters with predators are frequent and prevent digging for shells outside the colony (Kohler 1997). Females in a group compete for large numbers of shells (probably for future use by their offspring) and defend individual subterritories within the group against one another (C. Schradin and J. Lamprecht, unpublished results).

DNA analysis using three independent microsatellite loci (Kohler 1997) revealed that reproductive males were often close relatives, that some (11 of 41) adult females were possible daughters of the main reproductive (alpha) male, and that females produced offspring with their fathers or brothers. But there also was some evidence (unrelated males, unrelated females) suggesting eventual exchange of individuals between groups.

The evolution of the social system of *N. multifasciatus* raises several questions about the impact of intra- and intersexual conflicts and the factors that determine the outcome. We set out to investigate the following:

- (1) Do males and females differ in their propensity and/or ability to immigrate into foreign territories?
- (2) Can such sex differences, if they occur, be explained by different reactions of territory owners toward intruders of different sex? This would be the case if only one sex showed intrasexual intolerance. Yet intrasexual conflict might also be symmetrical, i.e., males expelling males and females expelling fe-

males, which would not explain eventual sex-biased immigration.

- (3) Can the males (as alpha males are always larger and stronger than their females; Kohler 1997) influence their females' aggressive behavior toward intruders? This would explain female-biased immigration. In another shell-dwelling cichlid of Lake Tanganyika, *Lamprologus ocellatus*, Walter and Trillmich (1994) found that males usually managed to maintain their harems of two hostile females by interfering in their agonistic interactions. In *N. multifasciatus*, too, this would (1) indicate an intersexual conflict over acceptance of members of a particular sex, and (2) show that males can express their own propensity toward polygyny against the females' rejection of competitors (probably for shells).

Methods

Fish, shells, and behaviors

The fish in the laboratory experiments were F1 and F2 descendants of wild-caught *N. multifasciatus* from a shell-bed population near Musende Bay at the southern end of Lake Tanganyika (Zambia). They were of different sizes and their ages were unknown. Before the experiments, they were kept in two 500-l tanks in groups of 60–70 individuals. The bottoms of these tanks were covered with a layer of fine white sand averaging 3 cm in depth. No shells were supplied in order to reduce territorial aggression. The experiments were performed in tanks of 234 l (65×60×60 cm), the bottoms covered with 3 cm of fine white sand. There was a 12:12 h light:dark schedule. During experiments, the fish were fed *Artemia nauplia* daily.

The standard length of each fish was measured (from the tip of the head to the end of the spinal cord; Nelissen 1992) and the sex determined by genital inspection (Kohler 1997). All fish were adult. Adult *N. multifasciatus* have dark-brown vertical stripes which immature fish lack. All fish could be recognized individually from variations in their stripe pattern.

All empty snail shells were imported from Lake Tanganyika and belonged to the species *Neothauma tanganicense*. Their height was measured as the maximum extension along the axis. The shells were placed inside a steel ring with a diameter of 25 cm. The ring was used to standardize territory size.

The following aggressive behaviors were recorded (Baerends and Baerends-van Roon 1950; Nelissen 1991; Lamprecht and Rebhan 1997): fast approach; display (corresponds to frontal and lateral display); tail-beating; pushing; biting, and mouth fighting. For each action, the actor and the recipient were recorded. When two or more individuals exchanged behaviors within less than 3 s, this was recorded as an interaction.

Statistics

Non-parametric tests were applied throughout (Siegel and Castellan 1988), and two-tailed *P*-values calculated. The term “Fisher test” is employed for Fisher's exact probability test, and “Wilcoxon test” for the Wilcoxon matched-pairs signed-ranks test.

Sex-biased immigration

The following experiments were performed to test whether male and female *N. multifasciatus* differed in their propensity and/or ability to immigrate into territories of pairs.

Field experiment

While scuba diving in a *N. multifasciatus* colony during October and November 1997 in the northern bay of Nkumbula Island at the southern end of Lake Tanganyika, we set up "immigration territories" of two types along the edges of the colony and at distances of 2 m or more from one another. For "old" territories ($n=6$), a marginal territory was chosen, which contained only one adult resident male and one adult female (in two cases, the second female was removed), and 7–10 shells of medium size (45–50 mm shell height) – to attain about 20 usable shells in each territory – were added to create an immigration incentive for neighbors. "New" territories ($n=10$), approximately alternating with "old" territories along the colony boundary, were created at less than 20 cm from the nearest colony territory (containing at least five adults) by digging out a depression in the sand and supplying it with 20 shells, many of them large (a height of >50 mm). In both types of territory, the shells were arranged with their openings above the sand. Daily checks and the final collection of all shells (and individuals) after 13 days revealed the number and types of individuals (and species) which had immigrated into these territories.

Statistical analysis was conducted at the level of territories, as immigration events into one territory are more dependent on each other than on immigration events into different territories.

Aquarium experiment

Fifteen pairs were established in experimental tanks, each pair with a territory of 20 shells. We used this large number of shells in order to reduce competition for them and increase the chances of immigration by strangers. An opaque PVC wall (34×25 cm) in each tank at a distance of 20 cm from the tank wall provided a hiding place for introduced strangers. The wall did not offer complete protection, as residents could also swim behind it.

Three days after a pair had been put into the tank and both fish proved to have become resident by staying inside the steel ring, a unfamiliar fish was introduced. As body size is an important determinant of dominance in fish (Barlow and Ballin 1976; Nelissen 1992), the chosen stranger was always smaller than the female of the pair, which again was smaller than her male mate. Thus, immigration success was made dependent on tolerance by the pair rather than dominance of the stranger. After the stranger had been added, observations were conducted on a daily basis until the stranger immigrated, but not for longer than 10 days. Ten pairs were observed twice daily for 30 min. The last five pairs were observed for 15 min once a day, because it had become clear by then that this was a sufficient interval to establish whether or not the stranger had immigrated. During the observation, the location of the stranger was recorded every 30 s. Three types of location were defined, with the head of the fish as the reference point: (1) within a snail shell, (2) inside the steel ring, but outside shells, (3) outside the steel ring.

A stranger was considered to have immigrated when it stayed in location type 2 on 3 consecutive days during at least 30% of the records. The criterion of 30% may seem insufficient, yet pair members also spent much time outside the steel ring, especially when digging, i.e., moving sand to the margin of the territory, and when defending the territory, which was in fact much bigger than the steel ring. All observed strangers spent either more than 30% of records in location type 2 (then termed immigrated or settled) or less than 10% – then interpreted as not (yet) immigrated. An additional criterion which had to be met by a successful immigrant was that during the 3 days with 30% of records in location type 2, both members of the resident pair were seen at least once outside their shells with the stranger, but not chasing it away.

After this first observation period, each pair was transferred to another tank with no shells but with other fish for 4 days to prevent it from achieving breeding condition [which would probably alter the aggressive motivation of the pair, as demonstrated in another shell-dwelling cichlid, *L. ocellatus*, by Walter and Trillmich (1994)]. After this break, each pair was put back into its tank. Three days later, another stranger (different in sex from the first one) was introduced as a potential immigrant. Observations were

made as in the first period. Each pair, in two different observation periods, was confronted with a male and a female stranger. For eight pairs, the first stranger was a male, for the other seven pairs, a female. The two strangers of a pair were of about the same size so that differences in immigration success could not be attributed to size differences ($P=0.473$, Wilcoxon test, $n=15$).

All interactions between the individuals were recorded. Behaviors (see above) were recorded as events, as it was not possible to record duration in interactions of three individuals. We also recorded how often the resident male interfered in aggressive interactions between the resident female and the (male or female) stranger. An intervention was defined as the resident male showing an aggressive act toward the resident female less than 3 s after she had attacked the stranger (strangers did not attack residents). For four pairs, no male interactions were observed, which reduced the effective sample size in the Wilcoxon test to 11.

Differences in aggression toward male and female strangers

A pair was established in each of 12 tanks. Each pair had a territory with 20 shells. For each pair, an unfamiliar male and an unfamiliar female of about the same size were chosen. Each stranger was used in all sessions with one pair only. The male and female strangers of a pair did not differ in size (Wilcoxon test, $T=30$, $n=12$, $P=0.432$). The male and female of each resident pair were tested separately to avoid mutual interactions (e.g., male interventions in aggressive female-female interactions, see above), by removing one partner in its shell to another tank.

Strangers were presented in a glass container (10 cm high and 8 cm in diameter on a 1-cm pedestal to prevent hiding on the bottom), which was placed adjacent to the steel ring surrounding the shells. An observation lasted 10 min and began when the territorial fish came out of its shell. The frequencies of tail-beating, pushing, and biting of the territorial fish were recorded as was the total time of display shown toward the stranger.

Eight tests were conducted with each resident individual, four with the strange male and four with the strange female (paired data). Data for each resident were later summed up both for the presentations involving the male and those involving the female stranger. Presentation of the strange male and female was alternated. Half of the fish were tested with a strange male, the other half with a strange female first. Each resident was tested only once a day.

For 2 of the 12 pairs, only the female could be tested as the male was too shy, i.e., he always remained in his shell during observation periods. Not all residents showed all aggressive behavior patterns. Thus, for some comparisons, the sample size in the Wilcoxon test was reduced due to the lack of response.

All comparisons were made with the Wilcoxon matched-pairs signed-ranks test. Standard Bonferroni adjustment of significance levels (Rice 1989) was applied when four measures of behavior were simultaneously tested in males or females. Significance levels of Wilcoxon tests are given as P , Bonferroni-adjusted significance levels as P' .

Male peace-keeping

Six groups consisting of two females and one male were established in experimental 234-l tanks, each group with a territory containing ten shells. Two sessions were staged for each group (paired data): during one session the male was in the territory, during the other he was removed (with his shell) and kept in another tank. Before observation with the male present, another empty shell was removed from the tank to keep confounding factors in the two sessions as constant as possible. In the first sessions of three groups, the males were present, in the first sessions of the other three groups, the males were absent. Observations lasted 30 min and began when all animals had emerged from their shells. All interactions between individuals were recorded.

After the second session, the male was removed from the tank permanently, and the following days were spent observing (for

15 min each day) whether or not both females remained resident in the territory. When one female spent less than 30% of the records inside the steel ring (and thus considered no longer resident), the male was replaced into the tank, and observations were made as to whether this female became resident again. The male-removal experiment was performed with an additional seventh group.

Results and discussion

Sex-biased immigration

Field experiment

N. multifasciatus immigrated into three of the six “old” territories (occupied by a pair) and six of the ten “new” (empty) territories. There was a significant difference between territory types in the proportion of territories with immigration by males ($P < 0.02$, Fisher test): “old” territories (three of three) experienced immigration by (one or more) females, never by males; “new” territories (six of six) experienced immigration by one or more males with or without females, and never by females only. The proportions of territories with immigrant females did not differ between territory types ($P = 0.50$, Fisher test), i.e., females immigrated into all three “old” territories, and into four of the six “new” territories with immigration.

Many of the “immigration territories” already contained new fish on the day after manipulation. Of the 25 immigrants finally collected, 8 were adult males, 11 were adult females, 1 was a (not fully striped) subadult female, and 5 were unstriped, but relatively large, juveniles of more than 17 mm standard length. No other juveniles were found in the “immigration territories.” Apparently, some adult *N. multifasciatus* group members do emigrate when opportunities become available; the demonstrated female bias in immigration could be due to the males’ lower tendency or ability to immigrate into territories already occupied by a pair. The first result precludes the possibility that the observed female bias in immigration is simply a consequence of a female-biased sex ratio [which was 94 females/66 males for the adult individuals counted by Kohler (1997) in 46 groups].

Aquarium experiment

Neither the male nor the female stranger immigrated into the territories of 5 of the 15 pairs and both strangers immigrated into the territory of one pair. This reduced effective sample size for the binomial test (testing whether male or female strangers immigrated more often into a territory) to nine. In one of these territories, only the male stranger immigrated, in eight of them, only the female stranger immigrated. This resulted in a significant predominance of female immigration into foreign territories (binomial test, $X = 1$, $n = 9$, $P = 0.04$). This result answers our first question, and demonstrates a higher tendency or ability of females compared with males to immigrate into a pair’s territory.

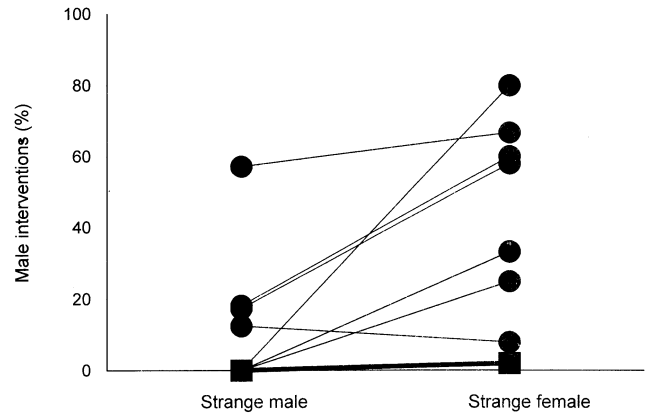


Fig. 1 Percentage of aggressive interactions by the resident female in which the resident male intervened. Interactions involving strange males are on the left, and interactions involving strange females are on the right. Values for each resident female ($n = 11$) are connected by a line. The filled squares and broad line represent four females with equal values

For 11 of the 15 pairs, the resident male was often observed to interfere in aggressive interactions between the female and the stranger, and the males interfered in a higher percentage of aggressive interactions of their females with strange females than with strange males (Wilcoxon test, $T = 9$, $n = 11$, $P < 0.05$; Fig. 1). This relates to our question 3, yet only shows the males’ differential behavior and not its effect on the females.

Differences in aggression toward male and female strangers

No habituation in the response toward the presented strangers was observed, probably due to the short presentation time. Territorial males displayed to strange males for significantly longer than to strange females ($T = 3$, $n = 10$, $P < 0.01$, $P' < 0.05$; Fig. 2a). The median against strange males was 117 s [first/third quartiles (Q): 73/322], against strange females 67 s (Q : 27/210). Males also showed more tail-beating against strange males (median: 0.5, Q : 0/1) than against strange females (median: 0, Q : 0/0), though not significantly so ($T = 0$, $n = 5$, $P = 0.062$); there were, however, no differences in the frequencies of biting ($T = 9$, $n = 9$, $P > 0.1$) or pushing ($T = 21$, $n = 9$, $P > 0.2$).

Territorial females showed more pushing against strange females (median: 4.0, Q : 2.8/8.8) than against strange males (median: 2.8, Q : 0.4/3.6; $T = 3$, $n = 10$, $P < 0.01$, $P' < 0.05$). They also displayed longer against strange females (median: 171 s, Q : 32/448) than against strange males (median: 112 s, Q : 19/333) and showed more tail-beating (median against strange females 2.0, Q : 0.8/8.0, median against strange males 1.2, Q : 0.4/2.4), though not significantly so (for display: $T = 7$, $n = 11$, $P < 0.02$, $P' > 0.05$; Fig. 2b; for tail-beating: $T = 4.5$, $n = 10$, $P < 0.02$, $P' > 0.05$), and there was no difference in the frequency of biting ($T = 9$, $n = 9$, $P > 0.2$).

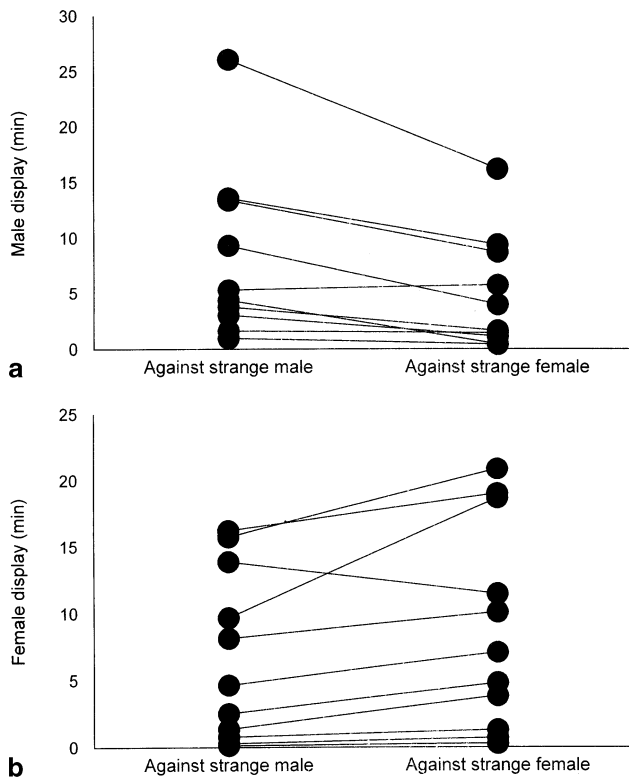


Fig. 2a,b Display (min in 40 observation min) shown by residents against strange males (*left*) and against strange females (*right*). The values of each resident are connected with a *line*. **a** Resident males ($n=10$). **b** Resident females ($n=11$)

Territorial females showed tail-beating against strange females more often than did their males, but the difference was not significant ($T=0$, $n=7$, $P<0.02$, $0.08>P'>0.05$). The median for females was 2.0 (Q : 1.2/8.0), for males 0 (Q : 0/0). There was no difference between mates in duration of display ($T=18$, $n=10$, $P>0.2$), frequencies of pushing ($T=18.5$, $n=10$, $P>0.3$) and biting strange females ($T=9$, $n=7$, $P>0.9$).

Territorial females showed more aggressive behavior against strange females, which are probably competitors for shells, than against strange males. Territorial males were more aggressive against strange males (reproductive competitors) than against strange females (additional mates). Territorial females were more aggressive than their mates against strange females, but this difference was not significant. The results suggest intrasexual conflict in both sexes, as mentioned in connection with question 2 (Introduction), but do not offer an explanation for the female-biased immigration observed in our first experiments.

Male peace-keeping

In our aquarium experiments on sex-biased immigration, males were shown to interfere in female-female aggression within their territory, and so the peace-keeping experiment (see Methods) was designed to test

whether female-female aggression is actually reduced by the presence of the male.

There were significantly fewer aggressive female-female interactions when the male was present than when he was removed (Wilcoxon test, $T=0$, $n=6$, $P<0.05$). The median of aggressive female-female interactions in the presence of the male was 0 (Q : 3/0), in the absence of the male, 4 (Q : 10/4).

If both females were resident in the territory independent of the presence of the male, they would be expected to remain resident after the male was removed. Yet in six of the seven groups, one female left the territory after male removal. This result differs significantly from the expectation that no female would be expelled (Kolmogorov-Smirnov one-sample test, $D=0.857$, $n=7$, $P<0.01$).

Males were put back into the six groups with only one female still resident in the territory. In two of these six groups, the male did not become resident again within the following 2 weeks (i.e., was never seen for more than 30% of the 30-s records within a 15-min observation period inside the steel ring). In these two groups, the second female also did not become resident again. In the other four groups, the male became resident again, and here the evicted females regained residence too. If females had left the territory regardless of male presence, they would not have been expected to regain residence upon male return, yet the result significantly differs from this expectation (Kolmogorov-Smirnov one-sample test, $D=1.000$, $n=4$, $P<0.01$).

General discussion and conclusions

Intra- and intersexual conflicts

In answer to the first question in the Introduction, whether there is a sex difference in the propensity and/or ability to immigrate into foreign territories, females proved more likely than males to immigrate into established groups in both the laboratory and the field setting. In the second question, we asked whether there is an indication of intrasexual conflict. In the temporary absence of their mates, resident females showed more aggressive behavior toward strange females than toward strange males, while resident males were more aggressive against male than against female intruders. Thus, there does appear to be intrasexual conflict in both sexes, which offers, however, no explanation for the female bias in immigration tendency. A conflict between the sexes, as addressed in the third question, was revealed when males interfered in female-female aggression by attacking the aggressor, i.e., the resident female. This male behavior was the likely cause of greater interfemale compatibility in the presence than in the absence of the male.

Fitness prospects for males and females

The reproductive success of a male is limited to a large extent by the number of females with which he can mate.

Therefore, additional females in a *N. multifasciatus* territory may constitute a reproductive advantage for the male.

Even in an artificial territory containing as many as ten shells and only two females, the residency of two females was often dependent on the male's presence. This suggests competition between females over some resource in the territory, and therefore fitness costs to a female through the presence of another female. The interpretation that the female who left the territory was not expelled by the other female, but was searching for a territory including a male for breeding, is very unlikely. In this case, both females should have left the territory. In the field, a female leaving a territory without emigrating at the same time into another (probably neighboring) territory is most likely to be eaten by a predator, due to the lack of a shell as protection shelter (Kohler 1997).

The males of a group provide no direct brood care for the young of a particular female. However, they defend the whole territory against predators and intruders, and remove sand from anywhere within the territory (indirect paternal care; for comparison between direct and indirect paternal care see Kleiman and Malcolm 1981). Thus male services are "nondepreciable" (i.e., do not decrease with an increasing number of applicants; see Clutton-Brock 1991, p. 8) and therefore cannot be a source of conflict. However, intact snail shells in the territory seem to be a "depreciable" resource, and we have behavioral evidence for the females' attempts to secure many shells (C. Schradin and J. Lamprecht, unpublished results). Surplus shells besides the home shell are probably future settling sites for a female's offspring. Initially, the young reside in their mother's home shell, yet after reaching a length of about 10 mm, each young starts to defend a shell of its own (U. Kohler, personal communication). The more females in a territory, the fewer shells will be available for the young of a particular female, hence the lower a female's reproductive prospects, as young without shells are likely to be caught by a predator sooner or later.

Conflict between the sexes on immigration of additional females

In our laboratory experiment with one female and 20 shells in a male territory, the resident females were much more aggressive than the males toward strange females. This difference between the sexes would be expected on the basis of the different fitness consequences of additional females.

Despite some possible benefits from "safety in numbers effects" or cooperation, males will gain extra profit through recruitment of additional mates and the optimum female number will always be lower for a female. Even if individual females lose a fraction of their reproductive prospects when new females settle, the total number of offspring produced in the group (and sired by the male!) may still increase. When this increase comes to an end, the male's optimum number of females is reached.

Similar to the findings of Walter and Trillmich (1994) in the (sometimes) polygynous shell-dwelling cichlid *L. ocellatus*, *N. multifasciatus* males were also capable of reducing the amount of female-female aggression, most probably by the observed male interventions.

Female-female aggression is also a common phenomenon in passerine birds, where it seems to reduce settlement of secondary females in male territories (Slagsvold et al. 1992, 1999; Kempenaers 1994; Karlsen and Slagsvold 1997; Iwasa and Harada 1998). Great tit (*Parus major*) females show a high degree of aggression toward a female presented in a cage. Females are more aggressive against strange females than against strange males (Slagsvold 1993). But while great tit females can prevent other females from settling and thereby defend a monogamous social system against the polygynous tendencies of their males, female-female aggression in *N. multifasciatus* is largely inhibited by male "peace-keeping behavior," which allows a polygynous social system in favor of the male's tendencies.

For female birds the critical resource seems to be direct paternal care and females that share their mate with another female receive less paternal care for their offspring and may have fewer surviving offspring (Pinxten et al. 1993; Kempenaers 1994). Analogous to Davies (1989) who pointed out that passerine females will resist settlement of additional females if their presence would lead to a decrease in reproductive output, we interpret the observed female-female aggression in *N. multifasciatus* as an indication of reduced female fitness when additional females settle in the male territory. For *N. multifasciatus* females, the critical resource seems to be the snail shells, probably as living quarters for future offspring. In the closely related, but not shell-dwelling, cichlid, *Lamprologus brichardi*, the critical resource for females also seems to be the quality of the territory, and not of the male, and thus female defense polygamy (Emlen and Oring 1977) is sometimes observed instead of the usual monogamous social system of this species (Limberger 1983).

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