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DIPLOMARBEIT

Polygyny in a predominately monogamous fish

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1. Introduction

In the animal kingdom we observe several mating systems, also in closely related species or species inhabiting the same habitat. This raises the question which mechanisms are responsible for these differences and how these strategies evolve. Whereas in different species various environmental and ecological constraints could exert their influence, different mating systems in the same species are the more puzzling. In various species, different mating strategies occur simultaneously, for example territorial courting males and “sneaker” males (Rios-Cardenas et al. 2007). Male fish can exert many strategies such as monogamy, polygamy as a harem leader or a satellite male (Martin & Taborsky 1997). To investigate costs and benefits of different mating systems, facultative polygynous species are a good choice, for example the longnose pipefish (*Oxymonacanthus longirostris*) or *Neolamprologus pulcher*. In *N. pulcher*, monogamous males are smaller than polygynous ones and had smaller territories, but obtained higher quality territories. However, in terms of brood survival, there were no differences between both strategies (Desjardins et al., 2008).

It is well known that male reproductive success increases proportionally with the number of matings, which makes polygyny usually beneficial for males. Males, and in a similar way females, face the trade off between increased mating opportunities and an increased investment in their first brood with sometimes marginal benefits. For example in lapwings, *Vanellus vanellus*, males mating with two females have a 58 to 100% higher reproductive success per breeding season than monogamous males due to fewer complete breeding failures (Parish & Coulson 1998).

Females on the other hand invest more in reproduction than males, as eggs are usually more expensive than sperm. Nest-site removal experiments in tree swallows *Tachycineta bicolor* showed that more aggressive females were more likely to obtain nesting cavities after the experimental reduction, while female age and male aggressiveness did not predict nest site

acquisition (Rosvall 2008). This means that for tree swallows, aggressive behavior during intrasexual competition over nesting sites between females is beneficial for critical breeding resource (Rosvall 2008).

In polygynous birds, reproductive success of females is often dependent on male parental care, and females may benefit from trying to prevent other females from settlement (Slagsvold & Lifjeld 1994). Females should prefer monogamy in all cases where paternal investment is not limited to sperm (Trivers 1972; Arnold & Duvall 1994). In species with bi-parental care, a female should choose her mate not only according to his genetic quality, but also consider his paternal abilities and should try to insist on monogamy. In many polygynous birds the reproductive success of females is strongly dependent on male parental care, and females mated with the same male will compete for a limited amount of male assistance (Slagsvold & Lifjeld 1994). Sandell and Smith (1997) examined the intraspecific aggressive behavior of breeding female starlings, *Sturnus vulgaris*. A breeding pair was exposed to a simulated intrusion of a caged conspecific bird (male/female). Caged females elicited stronger responses from females than caged males, paired females sang more often at the caged females than at caged males, and if the paired male had access to an additional nest box, the paired female was even more aggressive (Sandell & Smith, 1997).

Because polygamously breeding females have poorer reproductive success due to reduced male parental care in many bird species, intrasexual competition may be an important factor in the maintenance of monogamy (Slagsvold & Lifjeld 1994). Similarly in fish, monogamous females often behave aggressively towards an intruder female (Davies 1989; Trillmich 1994; Sandell & Smith 1997). For example, Walter (1991) and later on Trillmich (1994) observed strong female-female competition in *Lamprologus ocellatus*. Whenever two females simultaneously attempt to settle in a male territory usually the larger one settles first (Trillmich 1994). Males preferred larger females to breed with, and bigger females attacked smaller ones to acquire a breeding territory (Brandtmann et al. 1999). Therefore, smaller

females were unable to settle close to a larger one. Altogether, it is likely that larger females settled first due to male preference for larger females and intrasexual competition in females.

However, if female-female competition is not too strong and males acquire breeding territories of different qualities, the choice of females may be to settle on a good territory with an already mated male (Krebs & Davies, 1993). A model explaining the choice of this alternative mating strategies is the polygamy threshold model. It states that polygyny should evolve when females experience greater reproductive success by mating with an already mated male than with an unmated male. For example, monogamy will prevail if the variance in habitat quality is so small that females (and males) benefit more from breeding monogamously in a poor habitat than polygynously in a slightly better habitat (Björklund & Westman 1986). On the other hand, if a female is faced with the option to mate polygamously with a high quality male with a high quality territory or to mate monogamously with a low quality male with a low quality territory she will optimize her fitness by selecting polygamy (Ptak & Lachmann 2003).

The polygyny threshold model is based on five assumptions (Davies 1989; Orians 1969):

1. Sexes invest differentially in reproduction
2. Polygamy is costly
3. Reproductive success of mating pairs varies
4. The choosy mate can choose between potential mates and /or breeding habitats, and it is free to settle anywhere
5. Individuals optimize, over evolutionary time, their reproductive output

The polygyny threshold model is a compensation model, where the costs of sharing a male are compensated by gaining a high quality male in the best breeding situation. This compensation may be immediate through increasing the breeding success of that season, or may be delayed, by influencing future breeding success of the female or even the breeding success

of their offspring. The sexy son hypothesis can be seen as mechanism of indirect selection giving such delayed advantages (Alatalo & Rätti 1995).

Facultative polygyny for example occurs in longnose filefish, *Oxymonacanthus longirostris*. Monogamous pairs defend their territory which is a permanent feeding territory. However, occasionally polygyny occurs (Kokita & Nakasoma 2000), either when floater females settle at the beginning of a breeding season on a pair's territory (successive polygyny) or when a male annexes a neighboring territory after the male owner disappeared (replacement polygyny).

In this study we investigated if the usually monogamous, bi-parental cichlid, *Neolamprologus caudopunctatus* shows occasional polygynous mating and what the polygyny threshold of females may be. As long as the fish are unpaired, they form large, mixed-sexed schools which are mostly non-territorial. However, as soon as they form pairs, they start to defend their breeding site and subsequently the egg and fry. When *N. caudopunctatus* pairs have settled down at good breeding sites, they tend to breed very close to each other. Field observation show that a natural colony comprised over 130 breeding pairs while occupying less than 0.003% of the scanned area in otherwise unoccupied habitat (Schaedelin & Wagner, unpublished). All of these 130 observed breeding pairs were monogamous. However, in the aquarium under relaxed environmental constraints, fish were not strictly monogamous. In big tanks with lots of space to breed, it turned out that 1 out of 4 males managed to build a polygynous relationship by obtaining 2 females and 2 territories.

To identify a male quality measurement, we assessed in mate choice experiments if females of *N. caudopunctatus* preferred larger males over smaller ones, like in many other fish, for example the three spined stickleback (Roff 1992; Li & Owings 1978). Besides male quality, territory quality such as substratum type, depth or conspecific density, can have direct effects on juvenile growth and survival (Danilowitz 1997; Cheney & Côté 2003). Thus, mate quality as well as territory quality could play an important role in mate choice. Females mated with males who can secure territories richer in food and who are more attentive to

provisioning the nest probably have higher reproductive success than females mated to lower-quality males. Since the quantitative influences of the different factors on sexual selection are unknown in *N. caudopunctatus*, we combined both factors.

If polygyny is an option for female *N. caudopunctatus*, we expect that unpaired females choose the better mate with the better territory, even though he is already paired. Further, we predict increased female-female competition when the second female tries to get access to the paired male, as the paired female should try to impede a second pairing of her mate. Since the male probably benefits from an additional female, we do not expect to see any aggressive behavior of the paired male.

Predicting that females are probably choosier, I did two kinds of female choice tests: first, females could choose between two different kinds of territories which differed in size and breeding site quality; second, females could choose between an already paired male of high quality in a high quality territory or an small, poor quality male in a small territory.

2. Material and Methods

2.1. Study species

Neolamprologus caudopunctatus is a small (total length=6cm), sexually monomorphic cichlid fish endemic to Lake Tanganyika in Africa. *N. caudopunctatus* is one of the most abun-



dant cichlids in the intermediate habitat of Lake Tanganyika. It is a member of the species rich, substrate breeding cichlid tribe *Lamprologini*, which accounts about 40% of the lake's cichlid species (Sturmbauer et al. 1994, Stiassny 1997, Schelly et al. 1997). At many places, mostly in Zambian

Fig.1: *Neolamprologus caudapunctatus*

waters, large plankton-feeding schools can be seen. This species occurs as well in shallow water as well as in depths of more than 25 meters. They live in the intermediate habitat of the rock-sand interface. They prey upon many kinds of invertebrates from the substrate and mid-water (Koblmüller et al. 2007). Breeding takes place in rock crevices, as well as under pieces of rock on sandy bottoms, or even in empty snail-shells (Konings 1998). Pairs dig holes under stones to build their breeding cavities, whereby they transfer sand in their mouth (Ochi & Yanagisawa 1999). Clutch size varies between 100-250 eggs, which are stuck mostly on the bottoms of stones.

2.2. Housing conditions

We used 160 liter tanks as experimental and stock tanks. Focal females for the experiments were kept separately from males, whereas presentation females were kept in mixed sex tanks to stimulate pair formation and separate natural pairs. Day-night rhythm was 13:11 hours at a constant water temperature of 26° C. Fish were fed with dry food twice a week and 4 times a week with living artemia every morning before the experiments. The bottom of the tanks were covered by 3-4cm fine sand. Each fish was tagged individually: they got subcutaneous injections of different colors at different places, and depending on the color and the place of the marks, fish had their individual number, for example 124blue, 36red, etc (fig.2).

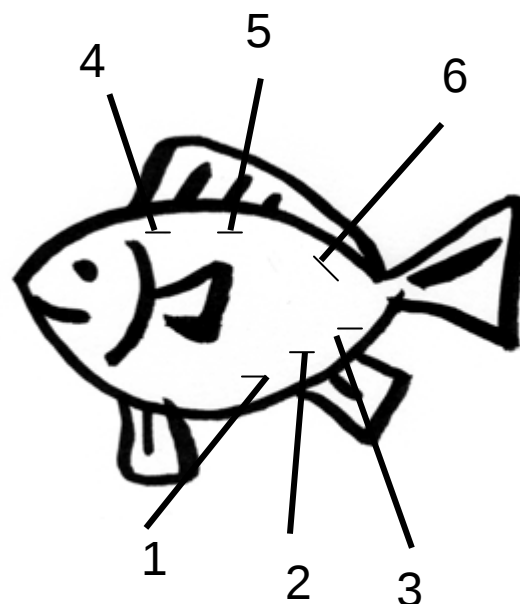


Fig.2: Method of individually marking the fish: arrows show which location symbolized which number

2.3. Habitat preference test

My first test was to find out if the females prefer big territories combined with a good possibility for breeding over small territories with a poor breeding shelter, in the absence of any other fish. For this experiment a tank was divided into 3 compartments: on one side the area was 15x40cm and included 2 snail shells, on the other side it was 45x40cm with two flowerpots. For compartment partitions we used a net, which allowed visual and chemical contact. In the middle compartment for the focal female (40x40cm), there were 2 extra dividers, 10cm away from the net, one on the side of the flowerpots reaching about half into the tank, one diagonally opposite also reaching halfway into the tank. These dividers marked the borders of the neutral zone and blocked visual contact between the two edge compartments. Around the tanks, I built a special hide with a curtain that people passing by could not disturb the fish.

I observed the focal female for a total of 60 minutes and noted every three minutes whether she was in the flowerpot preference zone, in the shell preference zone or in the neutral zone. Entrance in the preference zone was scored when at least half of the focal female's body had passed the non-transparent divider to a preference zone (Fig.3).

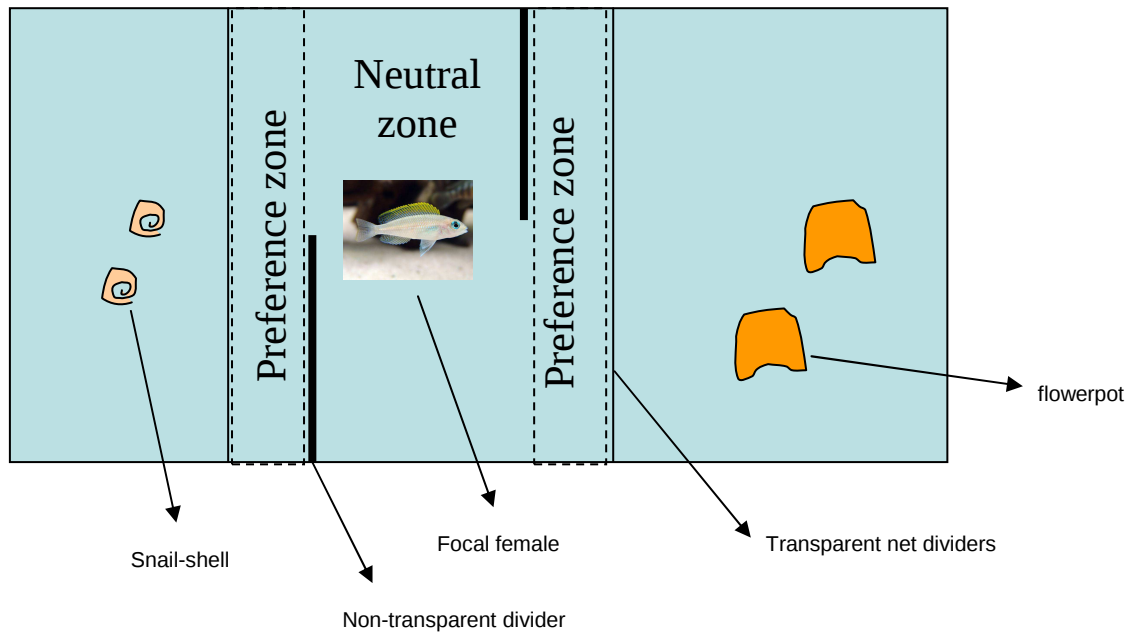


Fig.3: Set-up of the flowerpot-preference test: focal female in the middle compartment, which includes on the left and right side the two preference zones; on the right side: the compartment with flowerpots, on left side the compartment with snail-shells.

2.4. Mate preference test

For the mate preference test I used the same experimental set-up as for the preceding experiment. As before, I introduced one focal female in the middle compartment in each of my four experimental tanks. For the treatment I additionally introduced a single, small male in the small compartment with the snail shells and a female and a male paired up beforehand in the big compartment with the flowerpots (fig.4). A pair was considered to be together when they started at least 2 attacks within five minutes against other fish and began sharing some space in the mixed sex stock tank. The pairs and the single males were released into their compartments one day before the start of the experiment. Sides of the pair/single compartments were switched randomly, as were the locations of the non-transparent dividers (back of tank/front of tank). The male of the pair was always 10-15% bigger than the single male, and his female was always 10-15% smaller than the focal female.

For the control treatment, I introduced two small female fish in the pair compartment instead of a male-female pair. Here in the female-female pair used as control, both presenta-

tion females were smaller than the focal female in the middle. Each focal female was used twice, once for the treatment and once for the control, but always in a different tank and in the opposite side for the pair. The pairs (female or female/male) as well as the single males were exchanged for each trial.

The focal female was put into the tank 1 hour before the experiment began to allow her to acclimatize to the new conditions. The experiment started only after the female had visited both sides of the tank, the side with the single male and the side with the pair for at least 3 times.

The mate choice preference tests were recorded on video. I took 90 minute videos of all 20 control replicates and of the 20 treatment replicates by Geovision. Afterwards I scored the behavior of the fish on the computer with the help of the program “The Observer” from Nodlus Software. For each 90 minute observation, the frequency of the focal female swimming to the single fish and the group for treatment and the control were calculated.

I analyzed the following behaviors: the time and frequency the focal female had spent in the single preference zone, the pair preference zone or the neutral zone and the head down behavior and towards which fish (single or pair; time and frequency) it was shown (head down behavior means the fish swims with its head down). Whether a fish showed bars, a melanin pattern appeared on the body, consisting of dark, vertical bars. These patterns are shown by distressed or agitated individuals or when fish are at rest. Also I noted towards which fish (single or pair; time and frequency) the bar behavior was displayed. Further, the combination of the two former, head down and bars and towards which fish (single or pair; time and number). Additionally, I included the frequency and number of attacks and towards which fish (single or pair; frequency). As attacks was every kind of aggressive approach towards one of the other fish (frontal and lateral approaches, fast approaches with open mouth) classified. Finally, I investigated the behavior “insist” and into which compartment (single or pair; time and frequency) it was shown. Insists are attempts to enter a compartment – usual-

ly when the female swam up and down at the transparent net divider without any aggressive behavior.

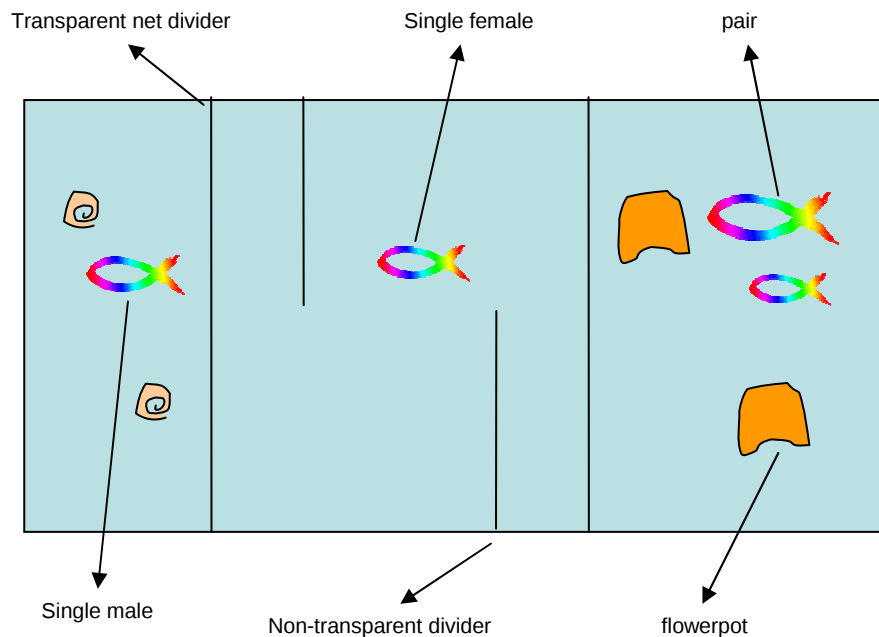


Fig.4: Set-up of the mate preference and female-female competition tests. The focal female in the middle can choose between a single male in a small compartment and the paired male in the bigger one.

2.5. Female-female competition

To investigate the individual behavior of all fish in the tank I did additional tests, where I observed them directly by sitting in front of the tanks. The set up was exactly as in the mate preference test. Each observation lasted for 60 minutes. I did 25 replicates with different focal females, single males and pairs. Five minutes before the observations started, I went into the hide with the experimental tanks and sat down quietly in front of the tank to give the fish some time to acclimatize to my presence.

Every three minutes I checked where the focal female was (neutral zone, with the single male, with the paired male or with the paired female) or if she showed a preference for another fish (which was noted down as “being with”). I noted down whether she showed any aggressive behavior towards any of the other fish and if she displayed head down and bars. I

did the same for the single male, the paired male and the paired female. Whenever the paired female focused on the paired male, I defined it as “being with paired male”, no matter if the paired male was also attentive to the paired female. So “being with” does not classify only mutual attention. I had no preference zones here; so when the paired female obviously followed the focal female or focused on her, the paired female was classified as “being with” the focal female, regardless of her location where in the tank.

2.4. Analysis

Statistical data were analyzed with SPSS 15.0. Most of the data were normally distributed (tested with K-S-Test for normality), and therefore I used paired t-tests for two sample comparisons. When data were not normal-distributed, I used Wilcoxon signed rank tests. For the correlations I did Bonferroni-corrections to correct for multiple testing.

3. Results

3.1. Habitat preference test

I made 25 observations of a single female choosing between a large territory with two flowerpots and a small territory with two shells. The mean time spent in the preference zone near the flowerpot was 30,68 minutes ($\pm 14,156$ min), mean time spent in the preference zone near the shell was 17,44 minutes ($\pm 14,402$ min) and mean time spent in the middle was 11,4 min ($\pm 11,376$ min). All data except time spent in the middle were normal distributed. The female spent significantly more time near the flowerpot territory than near the shell territory (paired sample t-test: $N = 25$, $t = 2,531$, $p = 0,018$). The female spent also significantly more time near the flowerpot territory than in the middle ($N = 25$; $Z = -3,445$; $p =$

0,001), but there was no significant difference between the time spent near the shell territory and the middle (N = 25; Z = -1,293; p = 0,196) (fig.5).

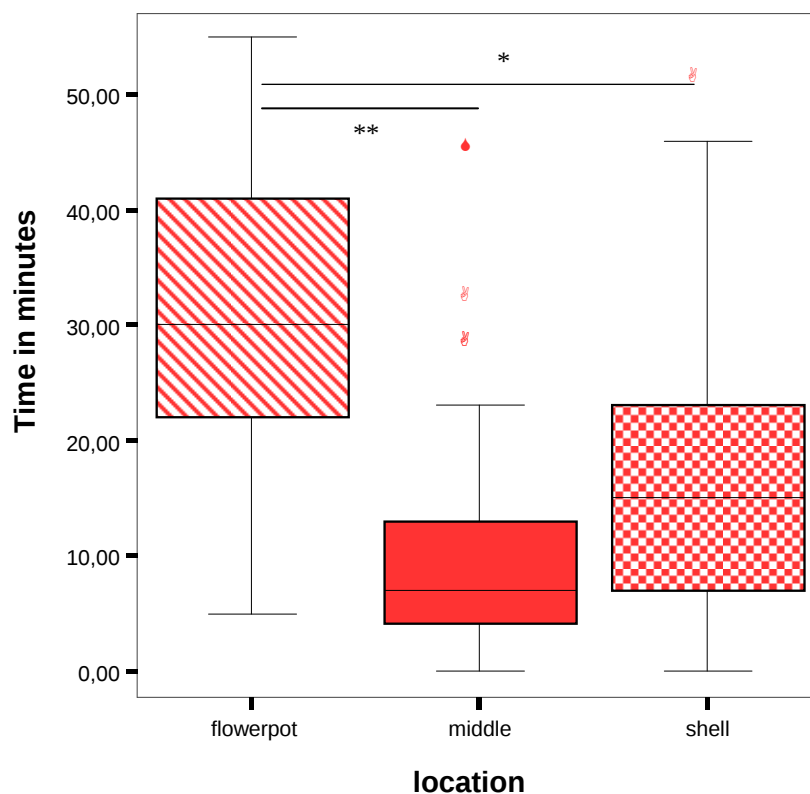


Fig.5: Boxplot of the time females spent in the different zones: y-axis time in minutes, x-axis shows zones, diagonal pattern= preference zone near flowerpot, red = middle compartment, checked pattern=prefeference zone near the shell; horizontal lines = medians, vertical lines and bars symbolize interquartile distances, stars and rings are extreme cases and outliers

3.2 Mate preference test

3.2.1 Frequency of swimming

For each 90 minute observation I recorded the frequency of the female fish swimming towards the single fish or the group. I had 20 replicates of each, the treatment and the control. Mean frequency of the female swimming towards the pair was 33,90 ($\pm 26,39$) and towards the single fish, 44,90 ($\pm 26,28$). In the control, mean frequency of the female fish swimming towards the single fish was 47,7 ($\pm 18,28$), and towards the two females was 46,35 ($\pm 23,5$).

All data were normal distributed. No significant differences were found with paired t-tests were (Treatment: N=20; $t = -1,201$; $p = 0,245$; Control: N=20; $t = 0,2$; $P = 0,843$) (fig.6).

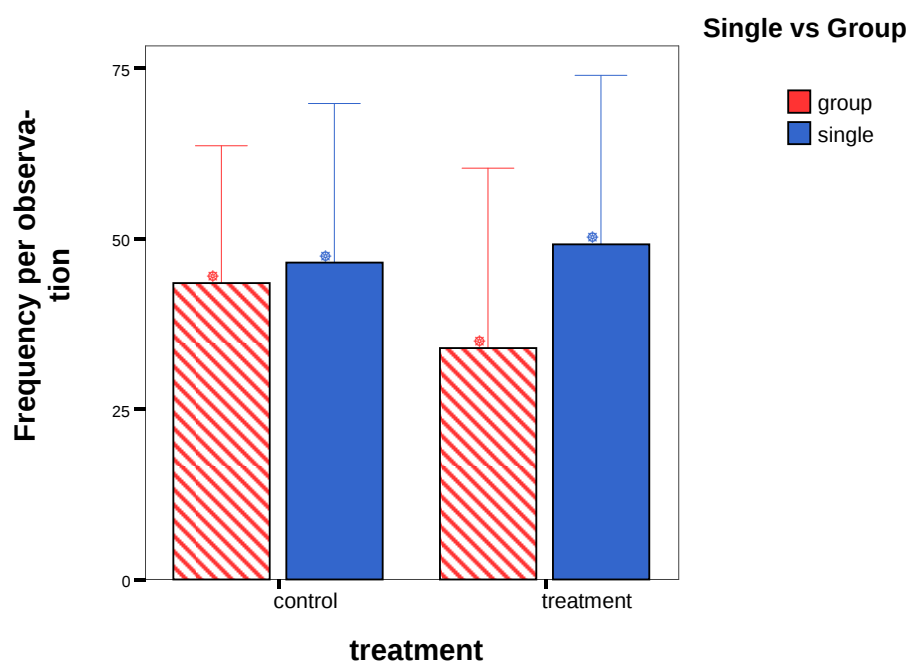


Fig.6: Frequency the focal female visited the different preference zones. Bars and error bars mean ± 1 SD; red patterned color shows behaviors towards the group; blue towards the single fish

3.2.2. Swim duration

I also calculated the swim duration, the time the focal female spent in both treatments either at the single fish or at the pair. In treatment she spent 6:09,9 min with the group ($\pm 6:05,9$) and 4:52,6 min ($\pm 4:06,05$) with the single fish. In control she spent 7:15,6 min with the group ($\pm 4:51, 3$), and 5:59,65 min with the single fish. All data were normal distributed. In paired samples t-tests no significant difference was found (Treatment: N=20; $t = 0,658$; $p = 0,507$; Control: $t = 0,658$; $p = 0,519$).

3.2.3. Frequency of insists

The average frequency of insists in the treatment was for the single fish 2,25 ($\pm 2,573$) and for the pair 4,05 ($\pm 5,643$); in the control group for the single fish 3,4 ($\pm 2,909$) and for the group 4,4 ($\pm 4,784$). All data were normal distributed, no significant difference was found in

paired samples t-test (Treatment: N=20, $t = -1,471$; $p = 0,158$; Control: N=20, $t = -0,958$; $p = 0,350$) (fig.7).

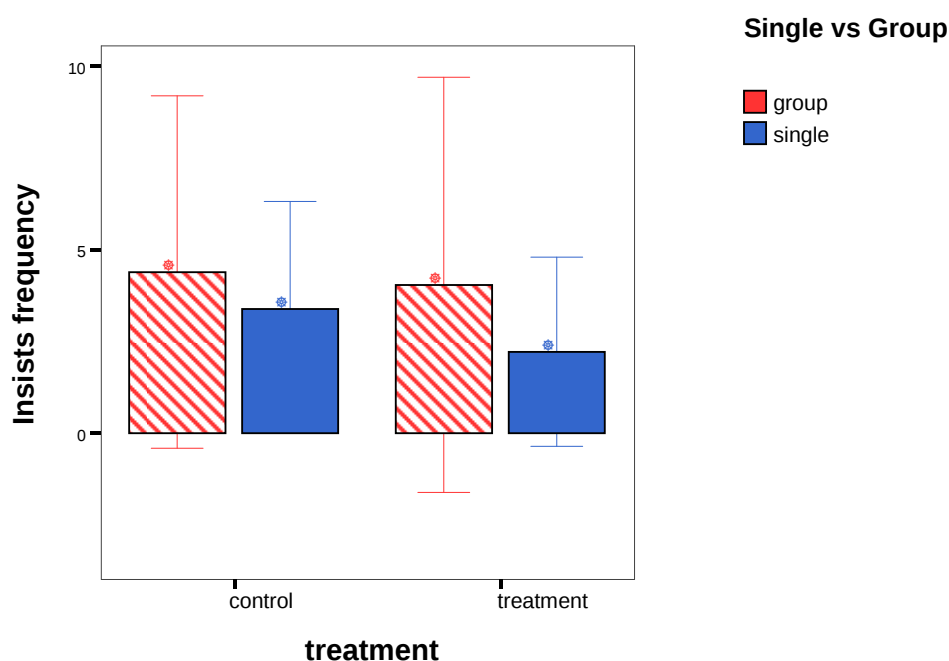


Fig.7: Frequency of insists of the focal female; red patterned = group, blue = single fish. Bars and error bars show Means $\pm$ 1,0 SD

3.2.4. Insists duration

The average duration of insists was in the treatment 20,10 sec (25,28) for the single fish and 37,05 sec (58,36) for the group. For the control it was at the single fish 23,65 sec ($\pm 29,36$) and for the group 31,05 sec ($\pm 47,88$). All data except the values for treatment-insist group were normal distributed. I used Wilcoxon Signed Rank Test for comparing the treatment-values, and paired samples t-test for the control groups, but no significant results could be found (Treatment: $Z = -0,414$; $p = 0,679$; Control: $t = -0,717$; $p = 0,482$).

3.2.5. Approach frequency

The average number in the treatment towards the single fish was 4 ($\pm 6,84$) and towards the group 5,55 ($\pm 7,67$). In the control, the mean number of approaches towards the single fish was 1,65 ($\pm 2,89$) and to the group fish was 9,4 ($\pm 17,05$). Only the treatment group approaches were normal distributed, so I did again Wilcoxon Signed Ranks Test

(Treatment: $Z = -0,739$; $p = 0,460$; Control: $Z = -1,735$; $p = 0,083$) (fig.8).

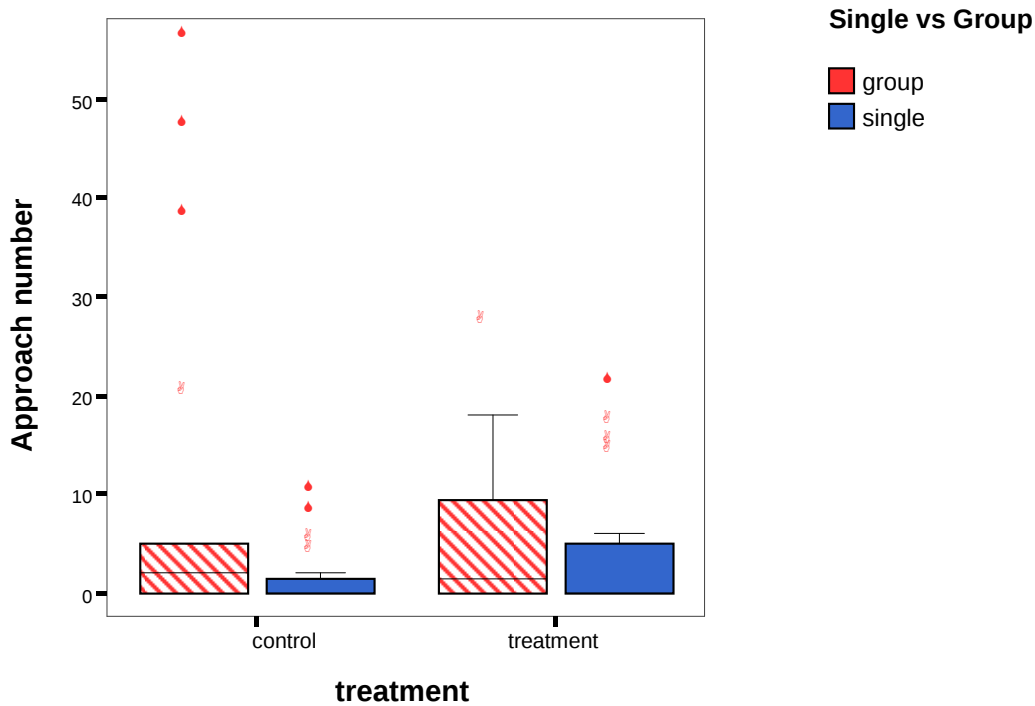


Fig.8: Boxplot for frequency of approaches of the focal female; red patterned = approaches towards the group, blue = approaches towards the single fish. horizontal lines = medians, vertical lines and bars symbolize interquartil distances , stars and rings are extreme cases and outliers

2.2.6. Head down bars

In the treatment the average number of head down and bar behavior was at 2,95 for the single fish ($\pm 5,55$) and 1,9 ($\pm 3,82$) for the pair. The average of head down-bars in control towards the single fish were 2,14 ($\pm 7,51$) and towards the group were 1,05 ($\pm 2,25$). None of these values were normal distributed; no significant difference found in Wilcoxon Signed Rank test (Treatment: $Z = -0,831$; $p = 0,406$; Control: $Z = -0,105$; $p = 0,916$)

2.3.7. Head down bars duration

The average duration of head down bars in the treatment was 37,2 sec ($\pm 13,71$) towards the single fish and 47,35 sec ($\pm 40,94$) towards the pair. In the control group it was towards the single fish 31,9 sec ($\pm 51,433$), and towards the group 12,80 sec ($\pm 27,03$). None of the

data were normally distributed, and the Wilcoxon Signed Rank test showed no significant difference between the groups (Treatment: N = 20; Z= -0,178; p= 0,859; Control: N = 20; Z= -0,169; p= 0,866).

3.3 Female-female competition

3.3.1. Locations

The focal female (f1) had been near the single male (m2) on average 4,28 times ($\pm 4,7$) within the 60 minutes. The focal female was 3,4 ($\pm 3,9$) times in the neutral zone and at the paired male (m1) 7,5 ($\pm 4,1$) times. She was 4,68 ($\pm 3,35$) times at the paired female (f2), which resulted in trying to enter the pair compartement 8,12($\pm 4,23$) times.. The paired female was 12,2 ($\pm 5,03$) times at the paired male, 7,8 ($\pm 5,03$) times at the focal female. The paired male was average 11,48 ($\pm 4,15$) times at the focal female, and 8,52 (4,16) times at the paired female. All data were normally distributed except the values for the focal being with the single male. The focal female was significantly more often with the paired male than with the paired female (N= 25; Z=2,512, p= 0.012). The paired female was significantly more often with her mate than with the focal female (N= 25; t=2,185; p= 0.039) (fig.9).

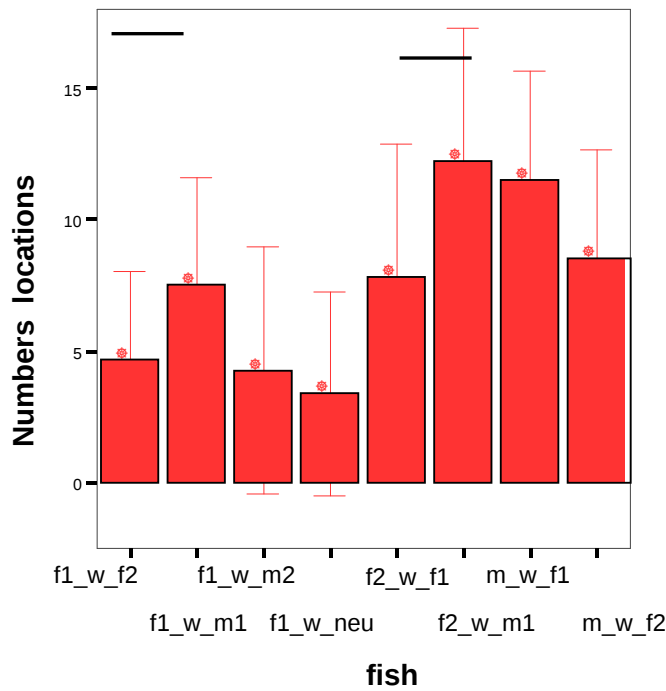


Fig.9: The frequency of “staying near with” of all observed combinations of fish. Bars show means and error bars show means $\pm$ 1,0 SD

3.3.2. Head down and bar behavior

The focal female did on average 0,96 times head down and bars towards the paired female ($\pm 1,46$), 0,52 times towards the paired male ($\pm 0,77$) and 0,64 (1,58) times to the single male. The paired female averaged 0,72 ($\pm 0,94$) times to the focal, and 0,44 ($\pm 0,65$) times to her mate. The paired male did average 0,8 ($\pm 1,0$) times to the focal female and 1,84 (1,55) times to his mate. Only the behavior of the paired male towards his mate was normally distributed. Wilcoxon Signed Ranks test indicated that the paired male made significantly more head down displays and bar behavior to the paired female than to the focal one ($Z = 2,373$; $p = 0,018$). The paired female showed a trend to perform more head down displays and bar behavior to the focal than to the paired male ($Z = 1,941$; $p = 0,052$) (fig.10).

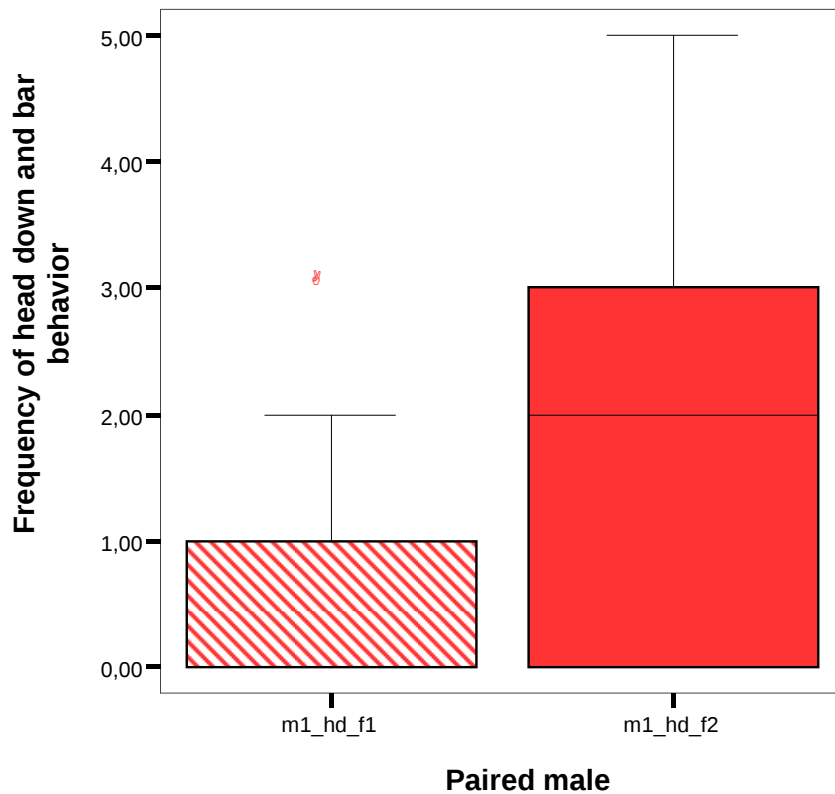


Fig.10: Boxplot of the frequency of head down display and bar behavior the paired male performed towards the two females: patterned towards the focal female, in red towards his mate; lines and bars symbolize interquartile distances; horizontal lines are the two medians; stars and rings are extreme cases

3.3.3. Aggressive behavior

The focal female showed an average of $7,32 (\pm 4,51)$ times aggressive behavior towards the paired female, $2,6 (\pm 2,08)$ times towards the paired male and $2,48 (\pm 3,84)$ times to the single male. The paired female showed $6,68 (\pm 4,79)$ times aggressions to the focal female and $2,6 (2,29)$ times to her mate. The paired male showed $2,16 (\pm 1,93)$ times aggression the focal and $2,36 (\pm 2,02)$ times to the paired female. All data except the aggressions by the focal female towards the single male were normal distributed. The focal female showed highly significantly more aggression towards the paired female than the paired male ($N=25$, $Z=5,008$, $p = 0,000$) (fig.11), and the paired female showed significantly more often aggressive behavior towards the focal female than to her mate ($N =25$; $t=3,607$, $\text{sig} =0,001$) (fig.12).

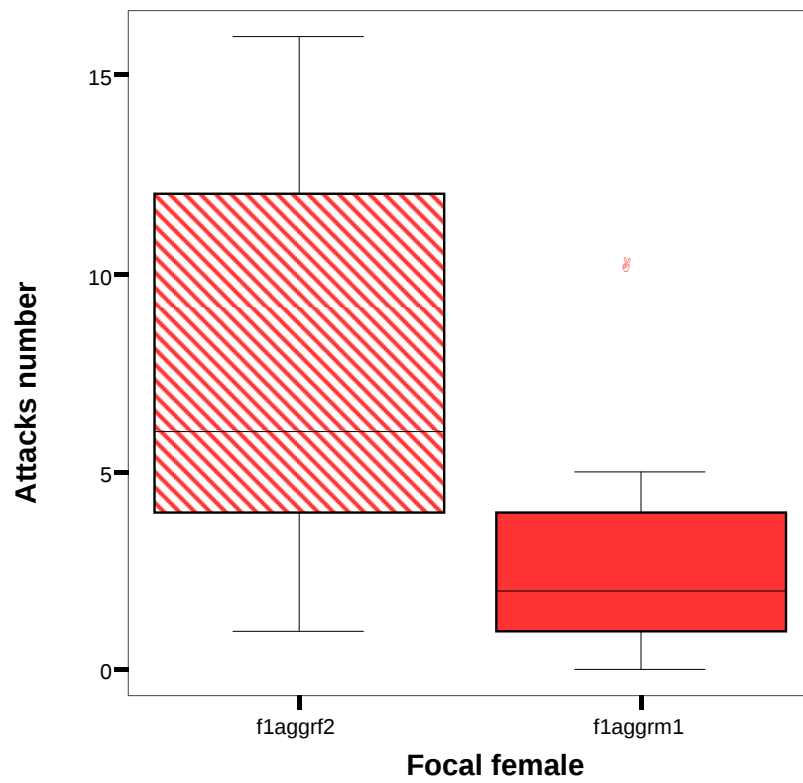


Fig.11: Boxplot of the frequency of attacks of female 1 towards female 2 (patterned) and paired male. ; vertical lines and bars symbolize interquartil distances ; horizontal lines are the two medians; stars and rings are extreme cases

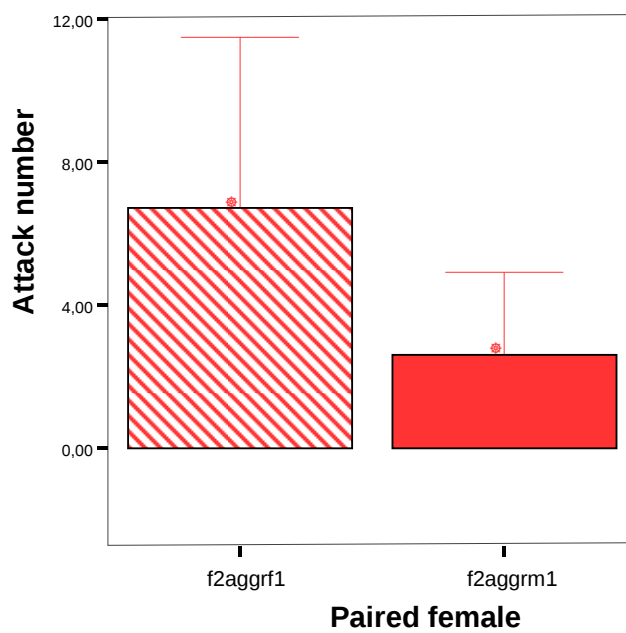


Fig.12: Numbers of attacks of paired female (f2) versus the focal female (f1) (patterned) and the paired male (m1). Bars show means and error bars show means $\pm 1,0$ SD

Comparing the behavior of the focal female towards the pair (male and female) and the single male, she significantly more often attacked the pair than the single male ($N=25$; $Z = -2,918$; $p = 0,004$).

3.3.4 Correlations

All correlations were done with a sample size of $N=25$. For the normal distributed data, I used Pearson correlations, for the others Spearman correlations. The behavior of the focal female with the pair female was reciprocal: The focal female increased the time with the paired one the more the paired one was with the focal ($r = 0,535$, $p = 0.006$). The more the focal female showed head down and bar behavior to the paired, the more the paired did so to the focal ($\sigma = 0,751$; $p = 0,001$). And the focal female showed significantly more often head down bars to the paired female the more often she was with the paired male ($\sigma = 0,737$; $p = 0.000$).

The paired female increased the head down bar behavior to her mate the more she displayed it to the focal female ($\sigma = 0,594$; $p = 0,002$), as well as when the focal female displayed it to her ($\sigma = 0,737$, $p = 0,001$). Additionally, the paired female displayed also more head down bar behavior to her mate, the more aggressive he behaved towards the focal female f1 ($\sigma = 0,543$; $P = 0,005$).

In the relationship between the focal female and the single male, aggression increased together with head down and bar behavior ($\sigma = 0,586$; $p = 0,002$). Similar was the relationship between the two paired mates: the more aggressive the male behaved, the more head down and bars he displayed to his mate (spearman $\sigma = 0,705$; $p = 0,001$). However, the situation was different for the relationship of the focal female with the paired male. In that the focal female displayed more head down and bar behavior the more she experienced aggressive behavior from the paired male ($\sigma = 0,543$; $p = 0,005$).

The more time the pair male spent with his mate, the more aggressively the focal female behaved towards the paired female ($\sigma = 0,494$; $p = 0,012$). And the less time the paired male spent with the focal female, the more aggressive she behaved towards him ($r = -0,494$; $p = 0,012$). With the paired female it was different. The less time she spent with her mate the more aggressive she behaved towards the focal female ($r = -0,793$; $p = 0,001$) (fig.13). Further, more time spent near the focal female increased the aggression towards the focal female ($r = 0,793$; $p = 0,001$).

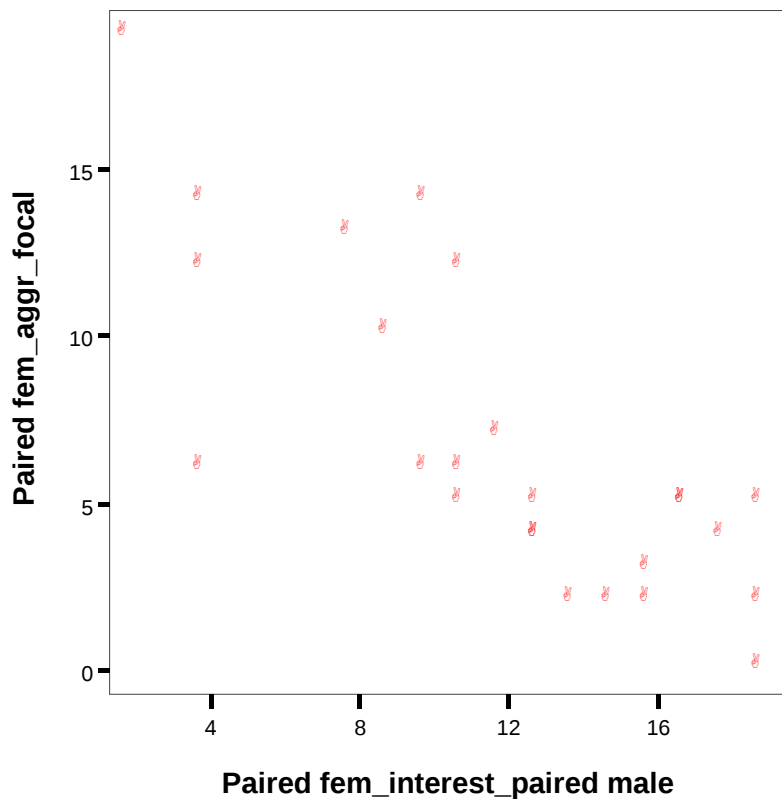


Fig.13: Correlation between the aggressiveness of the paired female towards the focal female and the paired female being interested in the paired male. The x-axis are the numbers of paired females showing interest in the paired male. The y-axis is the number of attacks of the paired female to the focal female.

The paired female was the more aggressive to the focal female the less the male was with her ($r = -0,694$; $p = 0,000$) and the more he was with the focal female ($r = 0,694$; $p = 0,000$).

The paired male behaved aggressively to his mate the more he showed head down and bars to his mate ($r = 0,780$; $p = 0,000$) (fig.14).

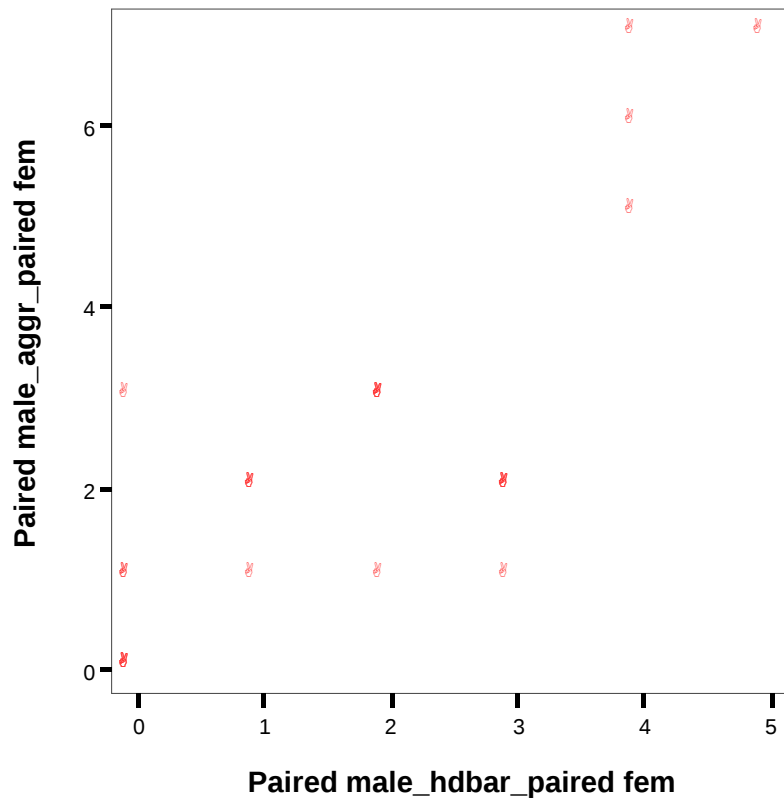


Fig.14: Correlation of the paired male being aggressive to paired female when he performed head down bar behavior to her. X-axis shows number of head down and bar behavior of the paired male towards his mate, the y-axis is number of attacks of the paired male towards the paired female.

The more the paired male attacked the focal female the more she was aggressive towards him ($r = 0,639$ sig 0,001).

4. Discussion

We expected that the focal female would prefer the more attractive male, independent of its pair status. Therefore, we predicted that the focal female would spend less time with the

unpaired, smaller male on a small territory. If the fitness of a female mating polygynously is greater than the fitness of a monogamous pair bond on poorer breeding site, females optimize their fitness by selecting polygamy (Ptak & Lachmann, 2003). However, during video observations we could not find any differences between the time the focal female spent with the pair and the single fish. Thus we could not show a potential polygyny threshold in *N. caudopunctatus*.

The costs of polygamy for the females may be very high because of reduced parental care, as the polygamous mated males share their attention between two broods. Thus, even if polygamous males are bigger and provide bigger territories, the benefits of being in a monogamous relationship might be much higher for females.

In this study, we tried to downsize all potentially significant mate choice cues for the single male, such as habitat quality and mate body size, but we do not know if there are some additional traits relevant for pair forming, for example dominance or ornaments, parasites or predation risk (Kvarnemo & Moore 2007; Berglund & Rosenqvist 2001; Berglund & Sandvik Widemo 2005).

Desjardins et al (2008) investigated the costs and benefits of polygyny in *Neolamprologus pulcher*, a closely related species. In this species, monogamous males were smaller, but they provided more parental care and better territories. On the other side, larger males are polygynous and provide less parental care in poorer territories. Thus female *N. pulcher* trade off male quality against paternal care and territory quality. One way females may resolve this dilemma is by obtaining extra pair fertilizations from high-quality polygynous neighboring males (Desjardins et al, 2008).

In *N. caudopunctatus*, we do not know if the amount of parental care changes when males are mated polygynously. But as there is usually bi-parental care, we would expect that instead of two parents providing parental care in a monogamous relationship, the male's attention is divided toward two females and their two broods. Yet, we expected that the

combination of a bigger territory and the bigger mate should be a good choice as we could show the female preference for each factor separately. First, females preferred larger males. In pre-experiments, we found that 6 out of 9 females chose the bigger male to spawn with. Second, females spent significantly more time on the side with two flowerpots in the bigger breeding area than in the flowerpot-shell trials. Therefore, we can conclude that females prefer bigger and better territories over small ones, in the absence of a potential mate. We do not know if females or males select territories before they are paired. I did not test if males show the same preference for a larger territory as the females. As my further investigations were focused on female interactions, I only tested females in these trials. In *L. ocellatus*, usually the females settle first, whereby the larger females can choose where to settle as the small females were unable to settle close to larger ones because of aggression (Brandtmann et al., 1999).

The focal female in the middle was able to choose in the control treatment between a pair of small females and a single male on the other side. We expected that the focal females would choose the single male in the control, because alternatively she could only join two small females. Yet, we found no significant preference for the single male in the control.

Apart from the explanation that the female did not seem to prefer the mated male on a better territory to the single male on a poorer territory, there are other alternatives. It could be that focal females would indeed prefer the paired male, but the pair female prevents this. In the focal trials, we found that test females spent significantly more time with the paired male than with the paired female, while the paired female was significantly more often with her mate than with the focal female. That shows the different interests of the two female fish. The focal female invests to get in contact with the paired male. She follows him, but he does not show a preference for either female. There is an interest from both females in the mated male, because at the same time, the paired female was more often with her partner than with

the focal female, as she followed her mate. Also the paired female was aggressive towards the focal female, independent of her behavior. Whenever one of the females was showing interest in the other, the paired female often behaved very aggressively to the focal female. She behaved also very aggressively when her mate was showing interest in her. However, surprisingly she was less aggressive the more her male and the focal female spend time together. On the other hand, when she was interested in her mate, she was less aggressive to the focal female. Thus, we found evidence for female-female competition which potentially prevented focal females from joining an existing pair. Mated females may benefit from trying to prevent or delay the settlement of other females as, for example, in many polygynous birds the reproductive success of females is strongly dependent on male parental care. Thus, similar to our fish model, female birds mated with the same male will compete for a limited amount of male assistance. For males, polygyny should be usually beneficial (Slagsvold & Lifjeld 1994; Trivers 1972). Hence, it is female aggression that may affect male mating success and thus play a role in the evolution of avian mating systems.

In video observations, focal females spent a little more time with the pair and performed more approaches towards it. However, for these observations, I could not differentiate between approaches towards the female or the male. Similarly, the number of focal females trying to enter a compartment, in video observations were usually slightly more for the group fish than for the single ones in both, control and treatment. *N. caudopunctatus* occurs mainly in large groups, so we would expect a preference by focal females to join the bigger group. These assumptions are confirmed by the fact that focal females spent little more time with the group fish than with the single ones, no matter if in treatment or in control. However, all these values did not turn out to be significant. One reason might be the limited sample size in combination with a large variance. For example, females seem to differ a lot in using head down bars. When fish show head down and bars, they get dark stripes on their back and swim with their heads down. There are some that virtually never show it, whereas others not even have to be stressed to get bars and swim head down. We have seen this be-

haviour in several distressed circumstances, for example during pair formation, in predation situations and in aggressive interactions.

Comparing all 25 focal-observations, the only significant value concerning head-down bar behavior was that the paired male displayed head down bars to his mate more often than to the focal female in the middle. I have two possible explanations for this: (1) It might be a sign of pair bonding or (2), appeasement behavior to reduce female-female competition.

Let's first explore to what extent pair-bonding plays a role here. In the beginning, we thought about the head down and bar behavior mainly as a signal for pair-bonding. Pairs starting to occupy a territory show head down bars to each other for long durations and several times a day. They swim next to each other or face to face and carry on for minutes. But even if the focal female attempted to pair with the already paired male, he would not have to do so. I did not try out what would have happened if I had removed the net between the focal and the pair compartments. Maybe there would not have been a polygynous pairing because the male would refuse to pair polygamously to avoid stress and aggressive fights between the females, which could his reproductive success. Alternatively, female-female competition excludes one of the females from the pair bond. When we set up 10 trios, only two were formed in which one was able to bring up fry by both females. There was usually one female that was chased away after several days. As though we selected both females with the same size, probably the tanks were small enough that one female was able to monopolize the male.

However, we could not find any correlations between the head-down bar behavior of the paired female and the paired male, and so they probably did not show it often to each other. That's why I suggest that it is rather 2) a sign for settling the dispute between the two females. Aggression was highest between the females (focal to paired average 7,32 attacks, to paired male 2,48; paired to focal average 6,68 attacks, to her mate 2,6), thus, it is really female-female aggression that occurred in my trials. For the male, it might be disadvantage-

ous to have two aggressive females around him and that is why he might have tried to settle that dispute by displaying head down and bars to his mate.

The more time the paired female spent with her mate, the more head down bars the focal female displayed to the paired female, either to show the paired female her aggression, or to show the male her motivation to pair with him. We give the first explanation more support as head down bars were mostly shown in combination with aggression. The fact that the more the paired male behaved aggressively towards his mate, the more head down bars he showed to her gives me the impression that head down bars is more involved with aggressive behaviors than with any sign of pair-bonding.

Also males show head down and bar behavior when they spot a possible intruder in their territory, in which case the behavior does not last long. In earlier experiments I could see females showing head down bars to their brood, I observed females showing head down bars while attacking another female or males while attacking females, and also females while attacking males. So head down bar behavior seems to be as well an inter- as intersexual cue. For me, it seems to be mostly combined with any kind of aggression, and the involvement in pair-bonding and showing that one fish belongs to another is rare.

The conclusion of these experiments is that even in monogamous species, competition among females happens like Trillmich (1994) and Berglund and colleagues (1993) have shown, and that also a normally monogamously pairing fish can be polygynous if the environmental conditions are different from the field settings.

What we know now about *N. caudopunctatus* can help us starting further investigations. Before starting all these experiments it was rather surprising to discover polygyny in this species. Now we should try to find out if breeding territories are really as clustered as we think, what causes the clustering of these territories, and which environmental factors limits their mating system to monogamy in nature. In my preliminary experiments, I tried to investigate mechanisms of aggregation as they are described in the hidden lek theory (Wagner

1997). *N. caudopunctatus* could be a good model species for it, because monogamous fish build their nests very close to each other like many seabirds. This species might be a perfect model species to investigate the hidden lek theory, because by choosing their breeding territories so close together, females might be able to gain extra-pair copulations by their neighbors.

Now we have to start experiments under semi-natural conditions to identify the key factors. We already did some trials and found out that probably, only in absence of a predator the males can obtain more than one female. When predators are present, the fish seem to be monogamous, so predation could be an important factor in enforcing monogamy in a species with flexible mating systems.

5. References

- Alatalo, R.V.,** Rätti, O. (1995). Sexy son-hypothesis controversial once more. *Trends in Ecology & Evolution* 10, 52-53
- Annold, S.J.,** Dvual, D., (1994). Animal mating systems: a synthesis based on selection theory. *Am naturalist* 143, 317-348
- Berglund, A.,** Magnhagn, C., Bisazza, A., König, B., Huntingford, F., (1993). Female-female competition over reproduction. *Behav. Ecol* 4, 184-167
- Berglund, A,** Rosenqvist, G. (2001). Male pipefish prefer dominant over attractive females. *Behav. Ecol* 12 402-406
- Berglund, A.,** Sandwik Widemo M., Rosenqvist, G. (2005). Sex-role revisited: choosy females and ornamented, competitive males in a pipefish. *Behav. Ecology*, 16(3), 649-655
- Björklund, M.,** Westman, B., (1986). Adaptive advantages of monogamy in the great tit (*Parus major*): an experimental test of the polygyny threshold model. *Animal behavior* 34 (5), 1436-1440
- Brandtmann, G.,** Scandura, M., Trillmich, F., (1999). Female female conflict in the harem of a snail cichlid (*Lamprologus ocellatus*): Behavioral interactions and fitness consequences. *Behaviour* 136, 1123-1144
- Cheney, K.L.,** Coté, I.M., (2003). Habitat choice in adult longfin damselfishes: territory characteristics and relocation times. *Journal of Experimental marine Biology and ecology* 287, 1-12
- Danilowicz, B.S.,** (1997). The effect of age and size on habitat selection during settlement of a damselfish. *Environ. Biol. Fishes* 50, 257-265
- Davies, N.B.,** (1989). Sexual conflict and the polygamy threshold. *Animal behavior* 38 (2) 226-234
- Desjardins J. K.,** Fitzpatrick J. L., Stiver K. A., Van der Kraak G. J., Balshine S. (2008). Costs and benefits of polygyny in the cichlid *Neolamprologus pulcher*. *Animal Behaviour* 75, 1771-1779
- Kobl Müller, S.,** Sefc, K.M., Duffner, N, Warum, M, Sturmbauer, C., (2007)
Genetic population structure as indirect measure of dispersal ability in a Lake Tanganyikan cichlid
Genetica Vol 130 (2), 121-131-

- Kokita, T.,** Nakasoma, A., (2000). Pair territoriality in the Longnose filefish *Oxymonacanthus longirostris*. *Ichthyological Research* 46, 297-302
- Konings, A.,** (1998). *Tanganyika cichlids in their natural habitat*. Cichlid Press, El Paso
- Krebs, J.R.,** Davies, N.B. (1993). *An introduction to behavioral ecology*. Blackwell Science Ltd, Oxford
- Kvarnemo, C.,** Moore, G.I., Jones A.G., (2007). Sexually selected females in the monogamous western Australian seahorse. *Proceedings of the Royal society of London, Series B* 274, 521-525
- Li, S.K., Owings, D.H.,** (1978). Sexual selection in the three spined stickleback II: Nest raiding during the courtship phase. *Behavior* 64, 298-304
- Martin, E.,** Taborsky, M., (1997). Alternative male mating tactics in a cichlid, *Pelvicachromis pulcher*: a comparison of reproductive effort and success. *Behav. Ecol. Sociobiol* 41, 311-319
- Ochi, H.,** Yanagisawa, Y., (1999). Sand-transfer behavior outside the nest by guarding parents of the Tanganyikan cichlid, *Neolamprologus caudopunctatus*. *Ichthyological Res* 46 (4), 419-422
- Orians, G.H.,** (1969). On the evolution of mating systems in birds and mammals. *American Naturalist* 103, 589-603
- Parish, D.M.B.,** Coulson, J.C., (1998). Parental investment, reproductive success and polygyny in the lapwing, *Vanellus vanellus*. *Animale behavior* 56, 1161-1167
- Ptak, S.E.,** Lachmann, M., (2003). On the evolution of polygyny: a theoretical examination of the polygyny threshold model. *Behavioral ecology* 14, 201-211
- Rios-Cardenas. O.,** Tudor, M.S., Morris, M.R. (2007). Female preference variation has implications for the maintenance of an alternative mating strategy in a swordtail fish. *Animal Behaviour* 74, 633-640
- Roff, D.A.,** (1992). *The evolution of life histories*. Chapman & Hall, NY
- Rosvall, K.A.,** (2008). Sexual selection on aggressivness in females: evidence from an experimental test with tree swallows. *Animal Behavior* 75, 1603-1610
- Sandell, M.I.,** Smith, H.G., (1997). Female aggression in the European starling during the breeding season. *Animal behavior* 53, 13-23
- Schelly, R.,** Salzburger, W., Koblmüller, S., Duftner, N., Sturbauer, C., (2006).

Phylogenetic relationships of the lamprologine cichlid genus *Lepidolamprologus* (Teleostei: Perciformes) based on mitochondrial and nuclear sequences, suggesting hybridization. *Mol. Phylog. Evol* 38, 426-438

Slagsvold, T., Lifjeld, J.T., (1994). Polygyny in birds: the role of competition between females for male parental care. *Am. Nat.* 143, 59-94

Stiassny, M.L.J., (1997). A phylogenetic overview of the lamprologine cichlids of Afrika (Teleostei, Cichlidae): a morphological perspective. *S.Afr.J.Sci* 93, 513-523

Sturmbauer, C., Verheyen, E., Meyer, A., (1994). Mitochondrial phylogeny of the Lamprologini, the major substrate spawning lineage of cichlid fishes from Lake Tanganyika in Eastern Afrika. *Mol.Biol.Evol* 11, 691-703

Trillmich, F. (1994). Female aggression and male peace keeping in a cichlid fish harem: conflict between sexes and within the sexes in *Lamprologus ocellatus*. *Behav. Ecol. Sociobiol.* 34, 105-112

Trivers, R.L., (1972). Parental investment and sexual selection. In: *Sexual selection and the Descent of Man* (Ed by B. Campbell), 136-179, Chicago Aldine

Wagner, R.H., (1997). Hidden leks: Sexual selection and the clustering of avian territories. *Ornithological monographs* Vol 1997, 123-145

Walter, B. (1991). Conflict of interest in a harem: behavioral observations on the snail cichlid *Lamprologus ocellatus*. *Steindacher 1909, Verh. Dtsch. Zool. Ges.* 84, 333-334

Zusammenfassung:

Im Tierreich kann man viele verschiedene Paarungsstrategien beobachten, welche von lebenslanger Monogamie bis zu Promiskuität gehen. Nach dem derzeitigen Stand der Wissenschaft ist es für Männchen meist produktiver, sich mit mehreren Weibchen zu verpaaren, und für Weibchen macht es mehr Sinn, einen Partner zu finden, der sich mit ihr um die Aufzucht des Nachwuchses kümmert. Dies liegt in erster Linie daran, dass Spermien weniger aufwändig zu produzieren sind als Eizellen, und der Reproduktion von Männchen im Grunde keine Grenze gesetzt ist.

Wir haben uns mit einer afrikanischen Buntbarschart aus dem Tanganjikasee beschäftigt namens *Neolamprologus caudopunctatus*. Diese Art siedelt auf meist sandigem Boden, und auffällig ist dass trotz ziemlich einheitlicher Substratgestaltung die Paarungsgebiete geklumpt sind, dh. viele Paare siedeln an einer Stelle, wogegen andere potentielle Brutreviere leer bleiben. Dennoch konnte beobachtet werden, dass die Tiere in der Natur monogam sind und die Jungen gemeinsam (paarweise) füttern und beschützen. Die Fragestellung war daher, warum es zu dieser Paarbildung kommt und ob es auch Polygynie geben kann.

Eine Annahme ist, dass Polygamie auch bei dieser Fischart unter Umständen nicht auszuschließen ist, und dass dies in erster Linie aufgrund des aggressiven Verhaltens der verpaarten Weibchen einer Konkurrentin gegenüber verhindert wird.

In verschiedenen Versuchen wurden Situationen geschaffen, um die Auswahl eines Weibchens zu testen. Dabei konnte ein in der Mitte eines Aquariums platziertes Weibchen (focal female) wählen, ob es ein kleines Männchen mit kleinem, schlechten Territorium bevorzugt oder ein sehr großes mit einem großen Territorium, welches allerdings bereits verpaart ist.

Um dies zu testen, wurde durch transparente Netze das Aquarium in 3 Teile geteilt, in welche die jeweiligen Fische gesetzt wurden. Es wurden verschiedene Verhaltensweisen beobachtet, wie Aufenthaltsdauer in den preference zones, Aggressionsverhalten, Head down Verhalten und die Versuche, ins benachbarte Areal zu kommen.

Zunächst konnte in einem eigenen Versuch festgestellt werden, dass die focal females ein großes Territorium einem kleinen vorziehen, auch ohne Anwesenheit eines Männchens. Weiters was bereits aus Vorversuchen bekannt, dass Weibchen große Männchen kleineren vorziehen.

Bei den darauf folgenden Tests ergab sich, dass focal females sich signifikant häufiger bei dem verpaarten, großen Männchen als bei seiner Partnerin aufhielten (selten beim kleinen Single Männchen), während die Partnerin sich häufiger bei ihrem Männchen aufhielt als beim focal female.

Die meisten Aggressionen gab es zwischen den beiden Weibchen. Die focal female zeigte sich signifikant häufiger aggressiv gegenüber der Partnerin des großen Männchens als gegenüber den Männchen selbst, und ebenso war das verpaarte Weibchen signifikant häufiger aggressiv dem focal female gegenüber als ihrem Partner.

Daraus zeigt sich, dass bei dieser Spezies tatsächlich female-female Aggression eine wichtige Rolle spielen dürfte für den Erhalt der Monogamie. In weiteren Experimenten soll nun unter naturnäheren Bedingungen herausgefunden werden, inwieweit Prädation einen Einfluss auf das Paarungsverhalten dieser Fischart hat.

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„Die Freiheit des Menschen liegt nicht darin, daß er tun kann, was er will, sondern das er nicht tun muß, was er nicht will.“

Jean-Jacques Rousseau

