# DIPLOMARBEIT

Titel der Diplomarbeit

## Colony formation and mate choice in
## *Neolamprologus caudopunctatus*

angestrebter akademischer Grad

## Magister der Naturwissenschaften (Mag. rer.nat.)

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# Abstract

Colonial breeding is a widespread phenomenon throughout the animal kingdom. Birds are well studied for colony formation, although colonial breeding can be found in many other taxa, e.g. fish. The aim was to test two hypotheses of colony formation. First, if breeding colonies form due to predation pressure to increase vigilance and dilution as a group. Second, if colony formation is a by-product of sexual selection. The Hidden Lek Hypothesis states that in a monogamous species less attractive males are forced by females to breed near a high quality male ("hotshot"), in order to obtain the possibility to trade up to the "hotshot" when opportunity is given. This mechanism can lead to the formation of colonies. I studied the monogamous cichlid *Neolamprologus caudopunctatus.* The study species performs bi-parental brood care and forms large breeding colonies in its natural habitat in Lake Tanganyika. Yet, the mechanisms that lead to these colony formations are not understood. I set up an experiment in a large Ring Tank providing semi-natural spatial conditions with equally distributed breeding cavities. Additionally, the study investigates mechanisms that influence the mating system of the study species, since facultative polygyny has been observed during the experiment, which is contrary to field observation. In general, monogamous mating is expected if females are widely distributed and males are unable to defend more than one female against other males. On the other hand, polygyny should be favoured if females are spatially clumped and males are able to defend multiple females from other competitors. The benefits of polygyny are obvious, since males are able to increase their reproductive success by fertilizing multiple females. Polygyny can also be beneficial for a female if mating with an already mated male enables access to a high-quality mate with a high-quality territory. Nevertheless, females face a trade-off between quality of their mate and parental care provided by the male.

Although our results revealed no answer to the question on mechanisms that lead to facultative polygyny, I found an influence of the presence of predators on the

behaviour of *N. caudopunctatus*. The study species breeds closer together under the presence of predators. Moreover, predation pressure initiates a higher parental investment in brood care and lowers reproductive success of pairs. Our results do not support the Hidden Lek Hypothesis since small males mated earlier when breeding solitary from large males considered as "hotshots". In addition, females did not divorce their mates if the chance was given to trade up to a larger neighbour. This is one of the few studies that experimentally show the direct influence of predation pressure on breeding colony formation.

# 1  Introduction

## 1.1  Colony formation

Colonial breeding, where individuals breed in densely aggregated territories, providing nothing else but nesting sites, is widely spread throughout the animal kingdom as marine mammals, reptiles and especially seabirds occur in colonies. Since decades evolutionary ecologists have investigated coloniality to find mechanisms explaining colony formation. They proposed several hypotheses, which will be discussed below.

The first hypothesis sees the benefit of colonies in enhanced food finding (Ward and Zahavi 1973). Food resources vary in quality and quantity as well as in time and space. It is essential for individuals to gain information about food locations for surviving, reproduction and rearing offspring. Birds that feed in flocks on an unevenly distributed food supply tend to roost communally whereas birds which feed solitarily on a variety of evenly distributed foods generally roost alone (Ward and Zahavi 1973).

The other well known hypothesis on colony formation is the benefit of reduced predation pressure in a group. Group living is a widely spread adaptation to predation pressure, which can be found in vertebrates (Clode 1993; Krause and Ruxton 2002) as well as in invertebrates (e.g. *Gammarus pulex*) (Kullmann et al. 2008). A mechanism that favours living in a group of conspecifics is dilution, whereby the individual's probability to be predated is reduced. Furthermore, individuals can decrease the investment in vigilance without suffering from a higher risk of an undetected predator attack (Krause and Ruxton 2002; Griesser and Nystrand 2009). Further, group defence is an important mechanism favouring group living. For example Picman et al. (2002) found that nesting sites in the centre of a breeding colony are safer than peripheral nesting sites in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*). They suggest that might be due to collective nest defence. Additionally, territories can be defended which could not be defended by a solitary breeding pair (Clode 1993).

On the other hand colonial breeding pairs can suffer from higher predation pressure compared to solitary pairs because predators detect groups easier (Krebs 1971; Dunn 1977; Varela et al. 2007). Furthermore, colonial breeders face considerable disadvantages like competition for food (Ballance et al. 2009), breeding sites and mates with other neighbours (Danchin and Wagner 1997) as well as parasite transmission, cannibalism and infanticide (Hausfater et al. 1986; Brown and Lang 1996).

Alternatively to the cost-benefit approaches above, two hypotheses explain breeding colony formation as a by-product of other individual preferences.

The habitat copying hypothesis suggests that birds use public information of conspecifics to estimate the quality of a breeding habitat (Valone and Giraldeau 1993; Danchin et al. 1998; Schjorring et al. 1999; Boulinier et al. 2002). Doligez et al. (2002) showed that public information on quality and quantity of offspring is used by conspecifics as an estimate for habitat quality in a field experiment on Collared Flycatcher (*Ficedula albicollis*).

The Hidden Lek Hypothesis on the other hand suggests a similar mechanism for colony formation as it is known for leks. Leks are aggregations of displaying males which females only visit for copulations. One of the three principal models of lek evolution is the hotshot model, which proposes that less attractive males aggregate near a high-quality male ("hotshot") to gain access to females that are attracted by the "hotshot" (Beehler and Foster 1988; Wagner et al. 2000). The Hidden Lek Hypothesis suggests that males of monogamous, colonial species aggregate their nesting territories by the same mechanisms that cause males of lekking species to aggregate their display territories. Thus females of monogamous species may prefer males with nesting sites near "hotshot" males in order to gain extra pair copulations (EPC), leading to the formation of colonies (Wagner 1993). Alternatively in species with no EPC, optimizing mate choice might lead to the same effect. In species with bi-parental brood care the female is dependent on her mate. As a result, the male is restricted to mate with only one female in order to assure reproductive success. This reduced availability of optimal mates due to monogamy might lead to suboptimal pair

bonds. Such pairs may settle near a "hotshot" pair and take the opportunity to switch to a more attractive partner if given the chance.

So far, hypotheses on colony formation have been mainly addressed in birds. However, breeding colonies can also be found in fish (Dominey 1983) where similar mechanisms might occur. Hence, the monogamous and colonial (Ochi and Yanagisawa 1999) cichlid *N. caudopunctatus* endemic to Lake Tanganyika was chosen as the study species. This fish performs bi-parental brood care and is relatively easy to keep in tanks, where experiments can be controlled in a very accurate way. In the experiment I exclude the benefits related to structure of the habitat and the enhanced food finding hypothesis by creating a uniform environment and feeding the fish ad libidum. I address questions on the benefit of reduced predation pressure due to colonial breeding, and colony formation as a by-product of sexual selection – the Hidden Lek Hypothesis.

## 1.2  Mating systems

Clutton-Brock (1989) points out three main ideas that provide the basis of animal mating systems:

1. Mating systems are not evolved specifications of species but the product of reproductive strategies of individuals (Bradbury and Vehrencamp 1977).

2. Social relationships lead to conflicts of interest between individuals, which result in diverse forms of competition. Conflicts of interest are widespread between mating partners (Davies 1985) as well as between parents and offspring (Trivers 1974).

3. Numerous mating systems represent different forms of mate guarding adapted to spatial and temporal distribution of receptive females (Bradbury and Vehrencamp 1976, 1977).

Monogamous mating systems, where both males and females limit the majority of their reproduction with one another are commonly observed (Kleiman 1977; Wittenberger and Tilson 1980; Bull 2000; Whiteman and Cote 2004). The occurrence of exclusive relationships still puzzles researchers, since males have a potential for higher reproduction if they mate with multiple mates. Hence, males

which mate with multiple partners should be favoured by selection (Clutton-Brock and Vincent 1991). Monogamous mating is expected when females are widely distributed and males are unable to defend more than one female against other males. On the other hand, polygyny should be favoured if females are spatially clumped and males are able to defend multiple females from other competitors (Emlen and Oring 1977; Kleiman 1977). Nevertheless, monogamy also occurs even if other unrelated females are in one territory (Lillandt et al. 2003; Stiver et al. 2005). Wong et al. (2008) suggest that females prevent other females from pairing with their mate. Additionally, competition for mates is triggered through limited resources (Wasser and Barash 1983; William 1987; Warner 1990), strong competition for suitable breeding sites (Borg et al. 2002), food and/or male care for offspring (Wasser and Barash 1983; Ali and Wootton 1999).

The benefits of polygyny on the other hand are obvious since males are able to increase their reproductive success by fertilizing multiple females (Orians 1969; Emlen and Oring 1977; Hasselquist 1998). Polygyny can also be beneficial for a female if mating with an already mated male enables access to a high-quality mate with a high-quality territory with many resources (Verner 1964; Verner and Willson 1966; Orians 1969). Nevertheless, females face a trade-off between the quality of their mate and parental care provided by the male (Webster 1991; Kempenaers 1994). For example in Red-winged Blackbirds (*Agelaius phoeniceus*), reproductive success is higher when nesting on over-water platforms. Females preferred to settle on the territories of mated males with over-water nesting platforms rather than on the territories of unmated males with over-land nesting platforms (Pribil and Searcy 2001). Furthermore, a female biased sex ratio which restricts the breeding opportunities for females has been suggested to favour polygyny (Smith et al. 1982; Kempenaers 1994; Pinxten and Eens 1997).

In *Neolamprologus pulcher* polygyny was impeded if males are able to provide essential assets but are unable to compete with larger neighbouring males for additional breeding positions. Polygamous males were larger than monogamous males. It seems that high quality breeding cavities are the major factor in

reproductive success as there was no difference in offspring survival between monogamous and polygamous groups (Desjardins et al. 2008).

In this study I have attempted to find mechanisms that favour facultative polygyny in a monogamous species.

# 2  Materials and Methods

## 2.1  Study species and housing

*Neolamprologus caudopunctatus* (Poll 1978) is a predominantly monogamous (Ochi and Yanagisawa 1999) but under lab conditions facultatively polygamous (personal observation) cichlid endemic to Lake Tanganyika. It lives in a rocky sub-littoral zone in 3-20 meters depth and hovers above the substrate to feed on zooplankton. Breeding takes place in rock crevices (Picture 1), as well as under stones on sandy bottoms, or in empty snail-shells (Konings 1998). Pairs build their breeding cavities by digging holes under stones by transferring sand in their mouth (Ochi and Yanagisawa 1999).

All fish in the experiments were caught between September and October 2006 near Mpulungu, Zambia or were from the F1-Generation.

The study species was kept in sex-separated tanks (400L), with a temperature of 26°C +/- 1 °C and fed with frozen food ( *Artemia sp.*, *Cyclops sp.*, red mosquito larvae, and *Daphnia sp.*), flakes for tropical fish and living *Artemia sp.*. Light was provided on a 13/11 hours light/dark cycle. Within one week before the experiment started three persons measured every fish's standard length (SL, without tail fin), total length (TL, with tail fin) and height (H, without fins). I took the mean of the values measured by three people. Each fish was weighted (W). To distinguish individuals during observation I used subcutaneous injections of Elastomere (Figure 1). Elastomere markers were provided by "North West Marine Technology".
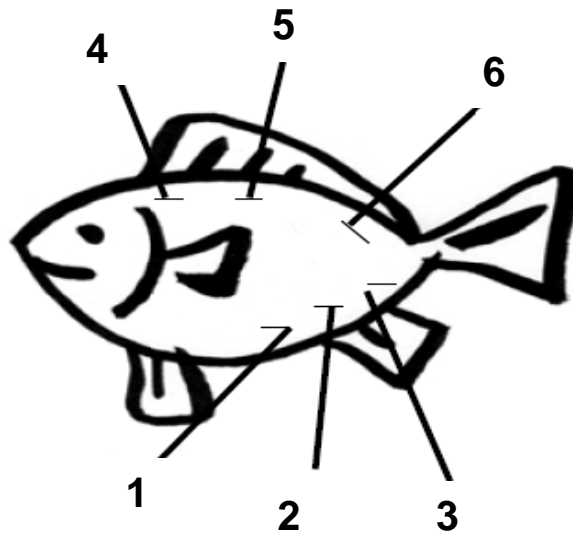
Figure 1: I used three locations next to the anal fin and three locations next to the dorsal fin for marking. Each location represents one number and by using different colours I was able to mark each fish uniquely.

## 2.2 Predators

In the "Predation" Treatment I introduced two different species of carnivorous fish from Lake Tanganyika. I combined two species of predators, one preying on adult *N. caudopunctatus* (*Lepidiolamprologus elongatus*) and one preying on eggs and fry (*Lamprologus callipterus*) to increase predation pressure and reflect natural diversity in predation.

- *Lepidiolamprologus elongatus* is a rock dwelling cichlid endemic to Lake Tanganyika (Boulenger 1906). Males grow up to 32.5 cm TL, females are little smaller than males. The carnivorous diet consists of fish and other small aquatic animals. For the experiments 10 juveniles of the F1-generation with a SL of 4 - 7 cm, a body size too small to threaten adult *N. caudopunctatus*, were used. The parental generation consisted of fish caught between September and October 2006 near Mpulungu, Zambia, Africa (Picture 2).

- *Lamprologus callipterus* is a snail dwelling cichlid endemic to Lake Tanganyika (Boulenger 1906). Females grow up to 6 cm TL and males to 15.4 cm TL. It feeds mostly on crustaceans and other invertebrates, but also on fish fry or eggs. For the experiments I used adult males sized between

10 – 15 cm TL caught between September and October 2006 near Mpulungu, Zambia, Africa (Picture 3). For each "Predation" Treatment 10 *L. callipterus* were randomly taken out of a pool of 25 individuals but not used in consecutive trials. The predators used in the experiments were caught between September and October 2006 near Mpulungu, Zambia, Africa.

Table 1: Number of fish used for each experimental trial as well as the ratio of wild caught and F1-Generation *N. caudopunctatus*. The following female groups were reused: Group 4 in round 7, group 2 in round 8 and group 3 in round 9. Three females from round 3 and one female from round 2 were used again in round 6. Males were only used once.

| | male *N. caudopunctatus* | | female *N. caudopunctatus* | | Predators | |
|---|---|---|---|---|---|---|
| round | wild caught | F1-Generation | wild caught | F1-Generation | *L. elongatus* | *N. callipterus* |
| 1 | 16 | 0 | 16 | 0 | 0 | 0 |
| 2 | 8 | 8 | 11 | 5 | 10 | 10 |
| 3 | 8 | 8 | 15 | 1 | 0 | 0 |
| 4 | 11 | 4 | 16 | 1 | 10 | 10 |
| 5 | 8 | 8 | 8 | 8 | 0 | 0 |
| 6 | 8 | 8 | 11 | 5 | 10 | 10 |
| 7 | 8 | 8 | 16 | 2 | 0 | 0 |
| 8 | 8 | 8 | 11 | 5 | 0 | 0 |
| 9 | 5 | 13 | 15 | 1 | 10 | 10 |
| 10 | 7 | 9 | 9 | 7 | 10 | 10 |

Table 2: Standard length (cm) of *N. caudopunctatus* used in each experimental round. "Small size class males" contains 8 smaller males. "Large size class males" contains 8 larger males. "Size females" contains all 16 females. Except for Experiment 4 were "Size small males" contains 7 smaller males and "Sizes females" 17 females.

| Experiment | small size class males | large size class males | size females |
|---|---|---|---|
| 1 | 4.22 - 5.12 | 5.77 - 6.17 | 4.15 - 5.50 |
| 2 | 4.60 - 5.42 | 5.48 - 6.38 | 4.41 - 5.67 |
| 3 | 4.52 - 4.92 | 5.55 - 6.17 | 4.58 - 5.70 |
| 4 | 4.37 - 4.80 | 5.05 - 6.03 | 4.13 - 5.53 |
| 5 | 4.15 - 4.77 | 5.62 - 5.98 | 4.42 - 5.58 |
| 6 | 4.57 - 4.92 | 5.48 - 6.05 | 4.33 - 5.95 |
| 7 | 4.55 - 4.90 | 5.07 - 6.18 | 4.35 - 5.50 |
| 8 | 4.50 - 4.98 | 5.30 - 6.05 | 4.92 - 5.67 |
| 9 | 4.53 - 4.82 | 4.83 - 6.20 | 4.80 - 5.77 |
| 10 | 4.35 - 5.50 | 5.75 - 6.02 | 4.63 - 5.55 |

## 2.3  Experimental Set up

I conducted the experiment in a ring shaped tank (Figure 2) comprising an undivided, full glass aquarium, 7.8 m in outer diameter that forms a torus with 16 corners. It is 1 m wide and 80 cm deep leading to a total water capacity of 16160 L. The Ring tank provides semi-natural spatial conditions and a shape that allows infinite swimming. The water temperature was 26 °C +/- 1 °C. The bottom was covered with a sand / gravel mixture at an average height of 4 cm. I equipped each compartment with 9 shelters as breeding opportunities for *N. caudopunctatus* (Figure 3). Grey PVC plates were bended in a 45 degree angle and placed inside the tank as shelters at the pane (Picture 4 & 5). Distances between shelters were 16 cm. I covered the shelters with black sheets from the outside, forming dark cavities within. To minimize disturbance, the Ring tank was surrounded by a wooden wall. The space between the wall and the tank was 60 cm. At the inside of the ring tank every other compartment was equipped with an outside filter allowing only to look inside by lifting up the filter material. The other compartments were covered with black foil on the inside leaving a space of 30cm between foil and aquaria.

I released 16 male and 16 female *N. caudopunctatus* simultaneously in the Ring Tank (one male and one female randomly per compartment). Predators were introduced dependent on the treatment before releasing the study species. None of the fish died during the experiments and were fed ad libidum once a day.
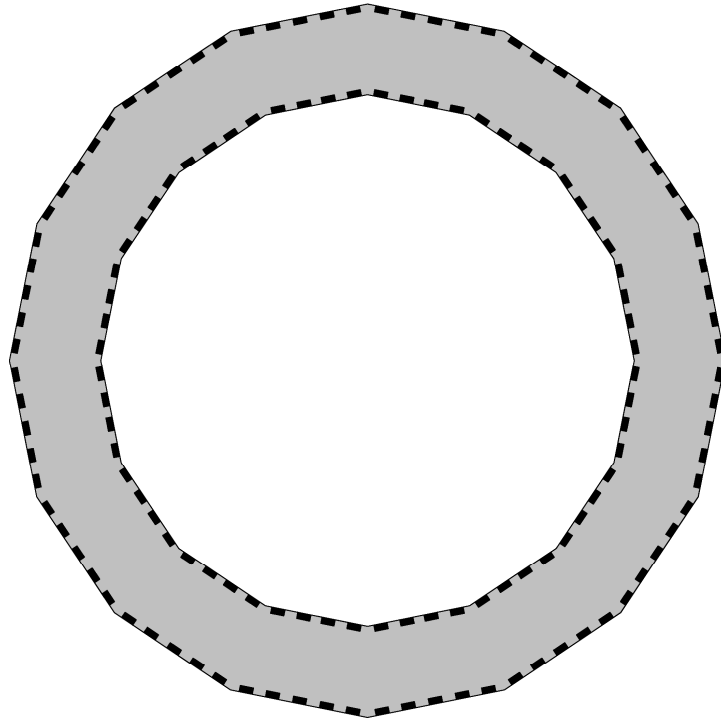
Figure 2: Schematic map of the Ring Tank. The black squares indicate potential breeding cavities and the sandy area without any structure is illustrated in grey.
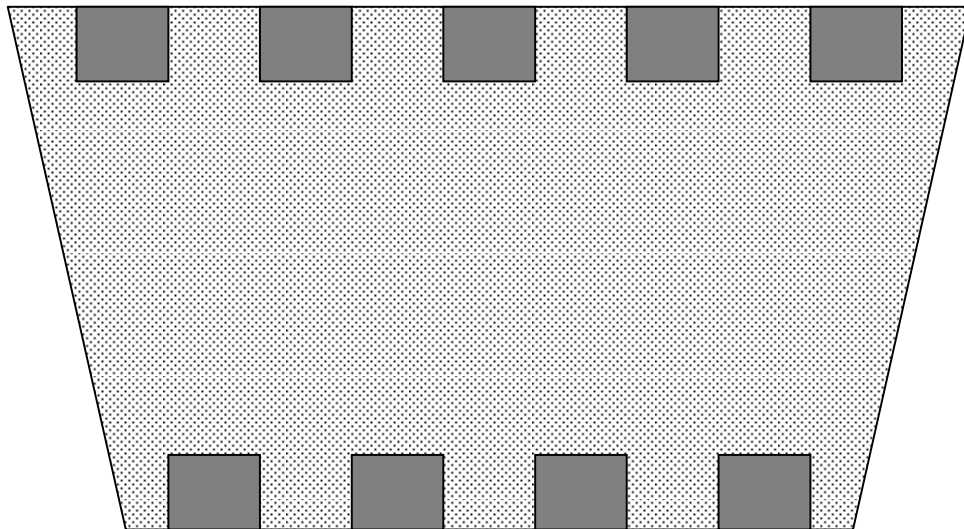


Figure 3: Schematic map of one compartment with shelters (grey area).

Picture 1: Colony of *N. caudopunctatus* in its natural habitat Lake Tanganyika (Photograph kindly provided by Stefanie Schwamberger).
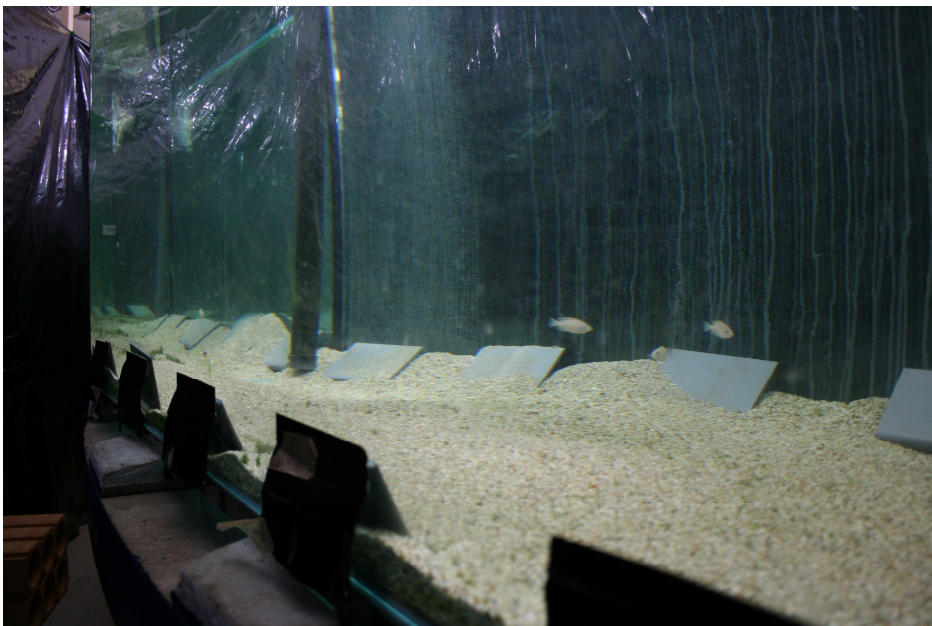


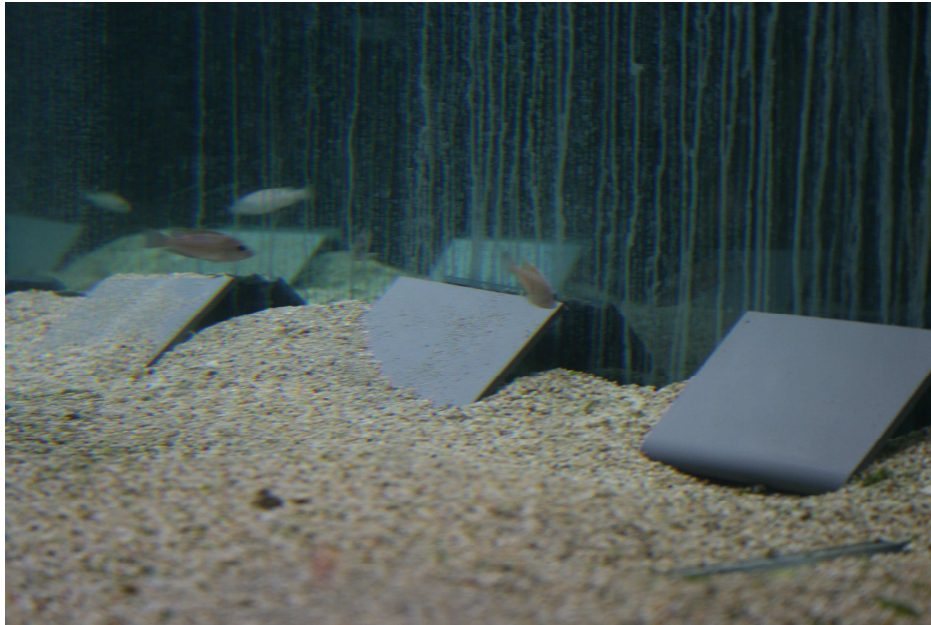Picture 2: A pair of adult *L. elongatus* in a stock tank (Photograph by Patrick Demus).

Picture 3: A male *L. callipterus* in a stock tank (Photograph by Patrick Demus).



Picture 4: View on one compartment of the ring tank during an experiment (Photograph by Patrick Demus).

Picture 5: Detail of the ring tank with three breeding cavities and a pair of *N. caudopunctatus.* The female is approaching the breeding cavity in the middle (Photograph by Patrick Demus).

## 2.4  Experimental procedures

On day 0 I introduced the fish according to treatment into the ring tank. I observed the cichlids every day until day 12. Each, day I made sure to identify every individual, recorded its position in the tank and checked for courtship activity indicating potential pair formations (Table 3). I exposed a potential pair to a one minute "intruder" presentation to confirm pair formation. Three juvenile conspecifics of mixed sexes smaller than the smallest fish in the experiment were placed in a transparent presentation tube. This tube was positioned in front of the breeding shelter. The acclimatization time ranged between 1 - 6 minutes and ended with the first attack of one of the focal fish. In the next minute each contact of a focal fish with the presentation tube qualified as an attack. I recorded number of attacks of the male, the female and both simultaneously. If both partners attacked the tube at least once during 1 minute of observation, they were considered to be a pair. If the presentation elicited no attacks, I conducted a different observation the next day. After 5 minutes of acclimatization, a 10 minute observation started. All behaviours

(Table 3) as well as the time the female stayed close to the nest (max. distance of 30 cm) and the time the pair spent together (max. distance of 30 cm) were recorded. If a male and female spent more than 50 % of the time together they were considered to be a pair.

Reproductive success was assessed daily by counting the number of eggs a pair produced. I counted the eggs on the first day they were laid 3 times in a row. If shelters were behind a filter chamber I could only recognize the eggs but not count them. On day 12 of the experiment I removed all eggs, larvae or fry. I removed eggs laid after day 12 of the experiment on the same day. I counted them once after exchanging the old for a new shelter. I measured the height of sand at the pane at both entrances of the breeding shelter to estimate nest building activity by the pairs, except for shelters that were hidden behind a filter.

## 2.5  Experiments

### 2.5.1  Colony formation experiment
I conducted 4 experimental rounds with a "Predation" Treatment and 5 experimental rounds with a "No predation" Treatment (Tab. 1). On day 12 in each trial I recorded all occupied breeding shelters by pairs. A 5th experimental round ("Predation" Treatment) was conducted during the time the data was analysed. Only the data on colony formation was used and the data concerning position of breeding cavities of small males with and without neighbours was analysed to increase the sample size.

### 2.5.2  Trading up experiment
On day 12 of the experiment or later I removed one paired female. If the focal male was polygamous I removed both females. I conducted a 10 minute observation with the abandoned male 24 hours after the removal to determine if the abandoned male paired up with a new mate. After this observation the removed partner was reintroduced again. 24 hours after reintroducing the removed female, I carried out another 10 minute observation with the focal male to determine if and with which female the former abandoned male was repaired. I kept removed females separately

in a tank (50 cm x 40 cm x 40 cm; 80 L) until reintroducing them into the Ring Tank. I did 4 female partner removals per experimental round (Tab.4).

### 2.5.3  Reproductive investment

I estimated reproductive investment with measuring the height of the sand piled up by the breeding pair in front of the entrances to the breeding cavities on the day eggs were laid. Reproductive success was estimated by counting the eggs that were laid.

### 2.5.4  Brood defence investment of polygamous males

I tested if polygamous males invest more in defending the breeding shelter of one of his two mated females. I conducted a double presentation if both females laid eggs. I simultaneously positioned the presentation tubes in front of the breeding shelters of the two females. The acclimatization time was one minute. In the next 2 minutes each contact of the three focal fish with one of the presentation tubes counted as one attack. After a break of 3 minutes, I swapped the presentation tubes and repeated the presentation. I recorded number of attacks by the male, the female and both simultaneously.

Table 3: All behaviours recorded during observations and daily checks.

| Functional context | Behaviour | Description |
|---|---|---|
| *Explorative behaviour* | *Visit shelter* | **Fish swims into shelter** |
| *Nest-building behaviour* | *Sand transfer out or in* | **The fish takes up sand into its mouth and carries it either away from the shelter (out) or to the shelter (in).** |
| *Con-specific behaviour* | *Head down* | **The fish swims head down and pauses in this position.** |
| | *Show bars* | **The normally beige fish shows a dark grey bar pattern on the body sides.** |
| | *Head down an show bars* | **The fish shows a grey to black coloration while swimming head down and pauses in this position.** |
| | *Lateral fin display* | **The fish erects its dorsal fin to full size.** |
| *courtship behaviour (towards partner)* | *Dive down* | **Approaching the potential partner, the focal fish dives down and lowers its tail while spreading gills and fins.** |
| | *Visiting shelter together* | **The two fish approach a shelter and swim in/through it.** |
| | *Head down* | **The fish swims head down and pauses in this position.** |
| | *Show bars* | **The normally beige fish shows a dark grey bar pattern on the body sides.** |
| | *Head down and show bars* | **The fish shows a grey to black coloration while swimming head down and pauses in this position.** |
| | *Lateral fin display* | **The fish erects its dorsal fin to full size.** |
| | *Swimming parallel* | **The potential pair swims parallel for at least 5 seconds with a maximum distance of 30 cm.** |
| *Defence behaviours (against con- or hetero-specifics)* | *Attack* | **The fish rapidly approaches another fish and touches it.** |
| | *Chasing* | **The fish follows another trying to attack it.** |
| | *Head down* | **The fish swims head down and pauses in this position.** |
| | *Show bars* | **The normally beige fish shows a dark grey bar pattern on the body sides.** |
| | *Head down an show bars* | **The fish shows a grey to black coloration while swimming head down and pauses in this position.** |
| | *Lateral fin display* | **The fish erects all fins dorsal fin to full size.** |

Table 4: An overview on which days in each round a removal was conducted.

|  | removals | | | |
| --- | --- | --- | --- | --- |
| round | 1st | 2nd | 3rd | 4th |
| 4 | 12 | 14 | 16 | 19 |
| 5 | 14 | 16 | 18 | 21 |
| 6 | 13 | 15 | 18 | 20 |
| 7 | 13 | 15 | 18 | 20 |
| 8 | 16 | 25 | 29 | 32 |
| 9 | 13 | 15 | 17 | 20 |

## 2.6  Statistical analysis

All statistical analysis was done using SPSS[©] 17.0 and Microsoft[©] Excel 2008. I tested for normality with the Shapiro-Wilk test. Data, where treatment was not considered, were analysed with Paired sample *t*-tests when normally distributed. Otherwise Wilcoxon signed-rank tests were used. Correlations were calculated with Pearson's correlation analyses if data were normally distributed. Otherwise Spearman's rank correlation analyses was used. To analyse the data of the double presentations, I used a General Linear Mixed Model (GLMM). Because of low sample size (N=10) I could not perform a backward stepwise removal procedure. I applied a forward stepwise addition procedure to avoid problems due to non-significant terms. I tested main effects and all two-way interactions one by one and in all possible combinations. To asses Aggregation I measured the distance between all breeding cavities in each trial. If breeding shelters were in one compartment I took the distance from one shelter to the other. If shelters were in different compartments the distance from the centre of the shelter to the middle of the boarder to the next compartment was taken. Then I added the distance through one compartment, multiplied with the number of compartments in between, and then from the middle of the border to the compartment with the breeding shelter to the centre of the shelter. A pair within a distance of 6 shelters is defined as a neighbour.

# 3  Results

## 3.1  Colony formation

The average distance between all breeding cavities on day 12 of the experiment differed significantly between the "Predation" and "No predation" Treatments (Mann-Whitney U Test: $N_1=4$, $N_2=5$, $Z=-2.449$, $p=0.014$; Figure 4)
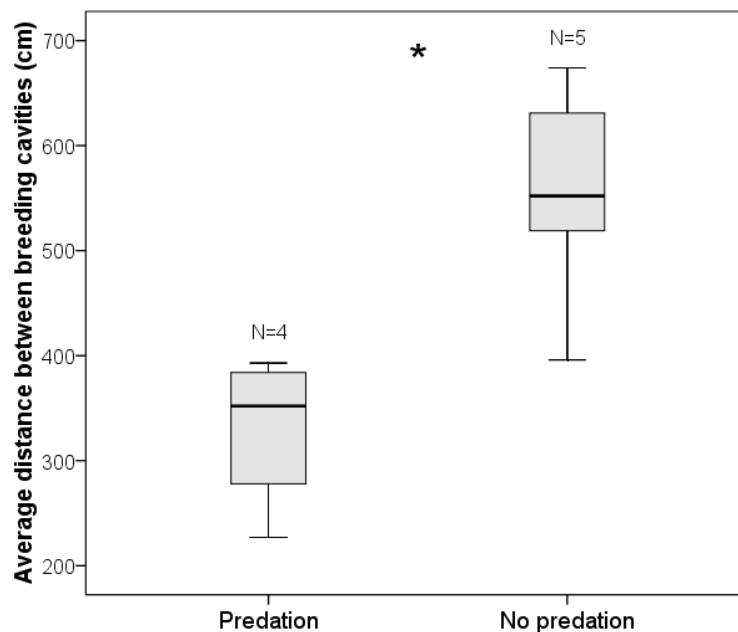


Figure 4: Average distance between all breeding cavities in both treatments on day 12 of the experiment. Horizontal lines are medians; boxes are upper and lower quartiles, whiskers indicate the highest and lowest values excluding extreme values and outliers. *: $p < 0.05$.

Males from the small size class obtained a mate earlier if they are without a neighbour than with a larger neighbour until day 12 (Mann-Whitney U Test: $N_1=6$, $N_2=12$, $Z=-3.120$, $p=0.002$; Figure 5). Males from the small size class without a large neighbour and with no neighbour did not differ in size (Mann-Whitney U Test: $N_1=6$, $N_2=12$, $Z=-0.281$, $p=0.779$) as well as their females (Mann-Whitney U Test: $N_1=6$, $N_2=12$, $Z=-1.136$, $p=0.256$; Figure 6) (10 Experiments). Out of 18 pairs, 14 were

formed during a "Predation" Treatment and 4 pairs during a "No predation" Treatment.



Figure 5: Day of pairing of males from the small male size class with or without a larger neighbour. Horizontal lines are medians; boxes are upper and lower quartiles, whiskers indicate the highest and lowest values, excluding extreme values and outliers. **: $p < 0.01$.

Figure 6: Standard length (SL) of females paired with males from the small size class until day 12. Horizontal lines are medians; boxes are upper and lower quartiles, whiskers indicate the highest and lowest values excluding extreme values and outliers. n.s.: not significant.

## 3.2 Trading up

It is more likely for males of the large size class than males from the small size class to re-mate (Fischer's exact test: N=28, p=0.011; Figure 7). When mates were removed from males belonging to the small size class, they did not get a new partner in most of the cases (Figure 7). Males from the large size class re-mated with a floating female in most of the cases (Figure 7). Re-mating pairs were similarly size matched as the first mated pairs: N=18, Wilcoxon Z=-1.254, p=0.210 (mean ± SD). In most of the cases after reintroducing the old female, males preferred to pair up with the old partner (Figure 8).
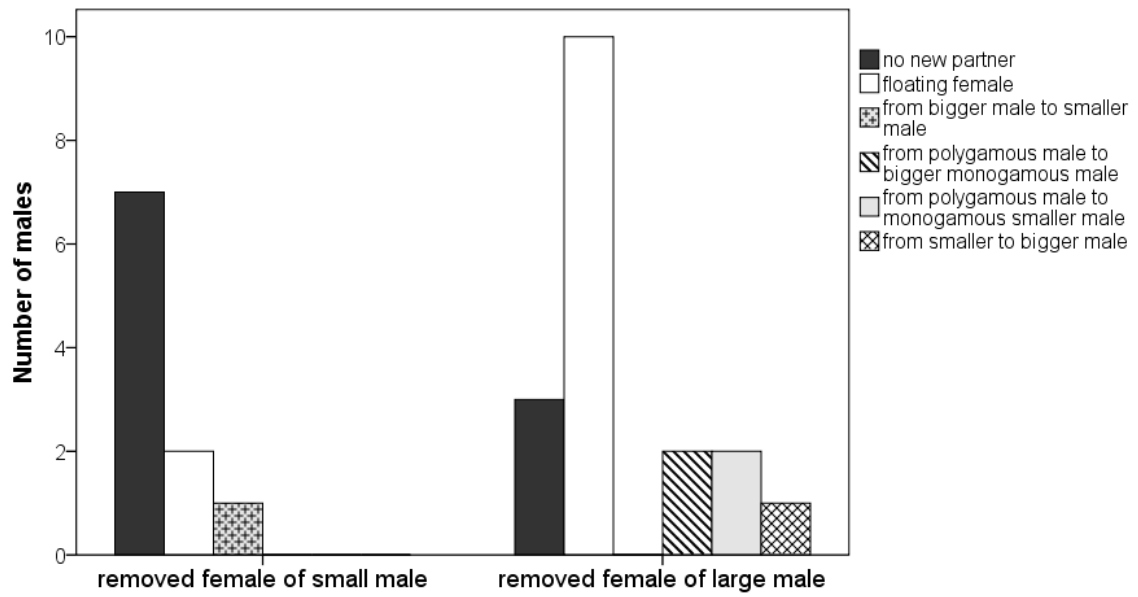
Figure 7: Outcome of the re-mating in numbers of males, categorized by pairing status of females before re-mating (N=28).
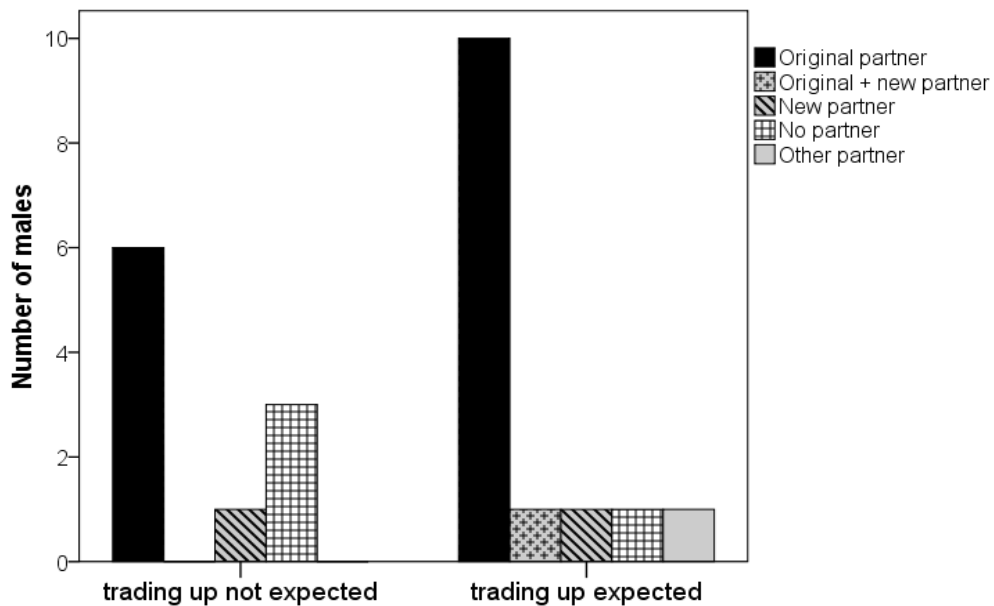
Figure 8: Mate of males 24 hours after the original partner, that was removed before, was reintroduced into the ring tank (N=24)."Trading up not expected" are males from the small male class. "Trading up expected" are males from the large male size class.

## 3.3 Reproductive investment

During the "Predation" Treatment pairs had piled up more sand at the entrance of their breeding cavities than in the "No predation" Treatment on the day eggs were laid (Mann-Whitney U Test: $N_1$=12, $N_2$=28, Z=-2.717, p=0.007; Figure 9). More than twice as many pairs laid eggs during the "No predation" Treatments (Figure 9). I found no relationship between standard length of males and the height of the sand pile on the day eggs were laid (N=35; ρ=0.137; p=0.431). The number of eggs being laid did not differ between the treatments ($N_1$=27, $N_2$=48, t=1.299, p=0.198, equal variances; Figure 10). However, there is a trend that females lay eggs later if predators are present (Mann-Whitney U Test: $N_1$=23, $N_2$=48, Z=-1.950, p=0.051; Figure 11).
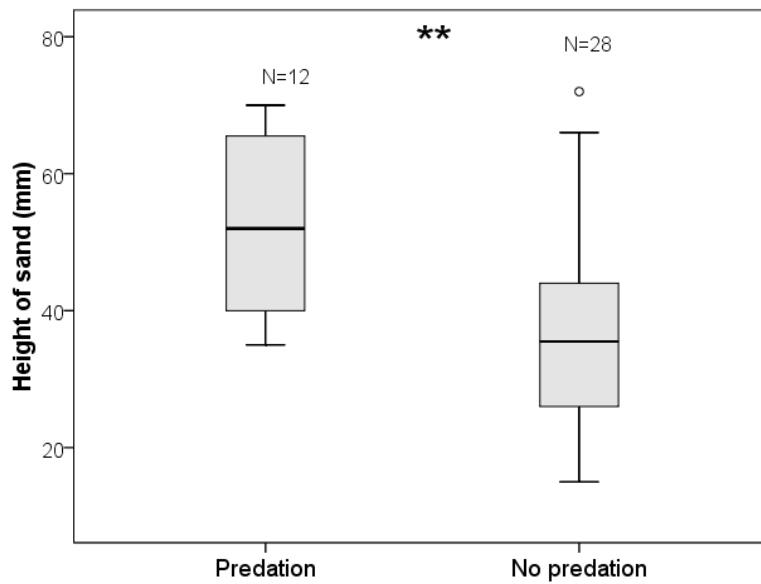
Figure 9: Height of sand at the entrance of breeding cavities on the day of egg laying (only males of the large size class). Horizontal lines are medians; boxes are upper and lower quartiles, whiskers indicate the highest and lowest values excluding extreme values and outliers. Open circles symbolize moderate outliers (between 1x and 3x interquartile range). **: p < 0.01.



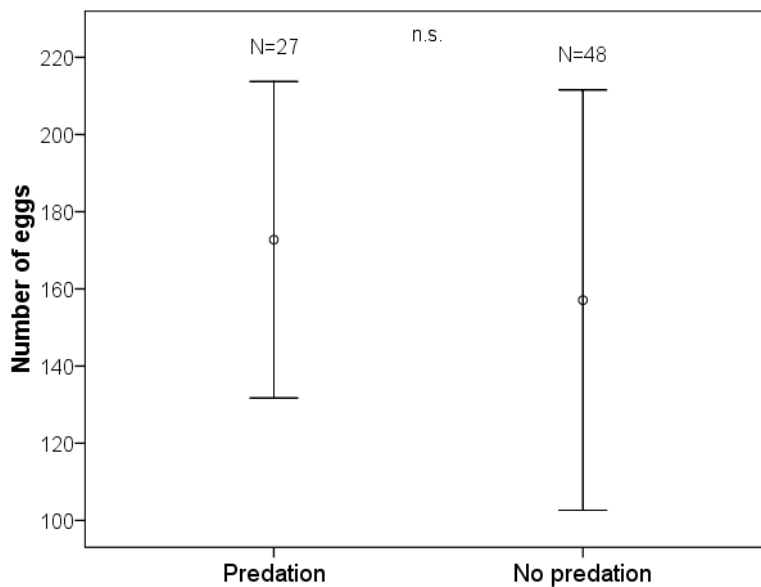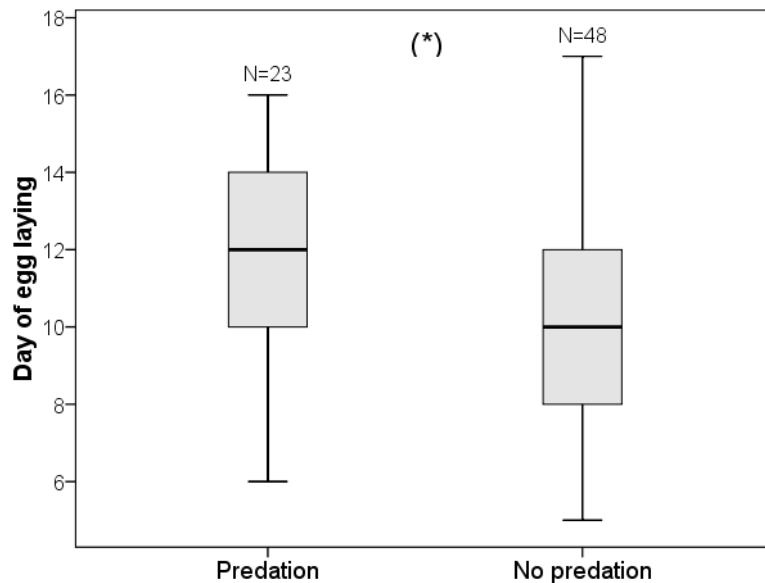Figure 10: Number of eggs laid in the two treatments until day 20. Mean ± 1 SD, n.s.: not significant.

Figure 11: Day of egg laying by females paired with males from the large size class until day 20 of the experiments in "Predation" and "No predation" Treatments. Horizontal lines are medians; boxes are upper and lower quartiles, whiskers indicate the highest and lowest values excluding extreme values and outliers. (*): $0,1 > p > 0.05$.

## 3.4 Mate choice

In the first 9 experimental replicates male and female *N. caudopunctatus* mated size assortatively (N=87, $\rho=0.484$, $p<0.001$; Figure 12). Also assortative mating by rank is significant (N=87, $\rho=0.466$, $p<0.001$; Figure 13).

The larger a male *N. caudopunctatus*, the earlier it pairs up with a mate (N=87, $\rho=0.466$, $p<0.001$; Figure 14). The speed of pairing does not correlate with the size rank of the male when separating into large male size class (N=66, $\rho=0.124$, $p=0.322$) and small male size class (N=21, $\rho=0.028$, $p=0.904$). Floating females are not smaller than paired females (Mann-Whitney U Test: $N_1=97$, $N_2=48$, $Z=-0.973$, $p=0.331$).

Within the small size class, larger males were more likely to obtain a mate ($N_1=21$, $N_2=50$, $t=3.056$, $p=0.003$, equal variances; Figure 15).
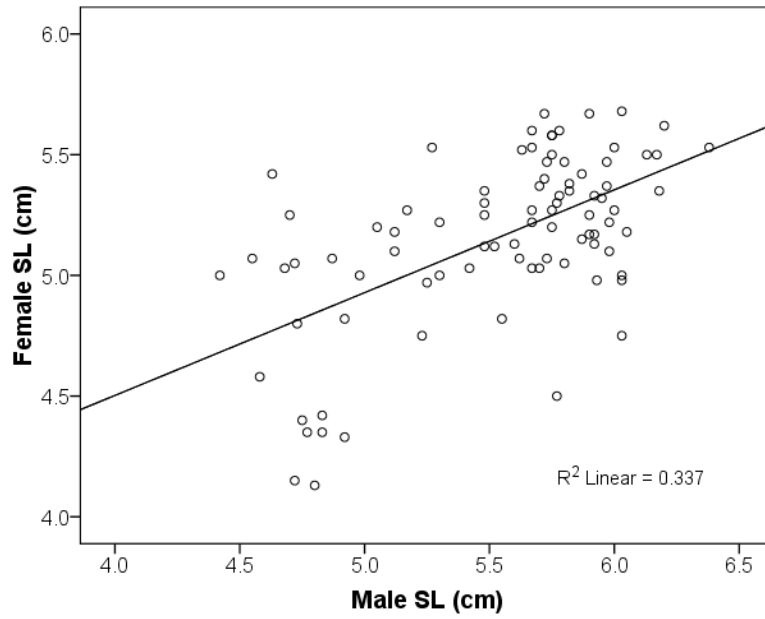
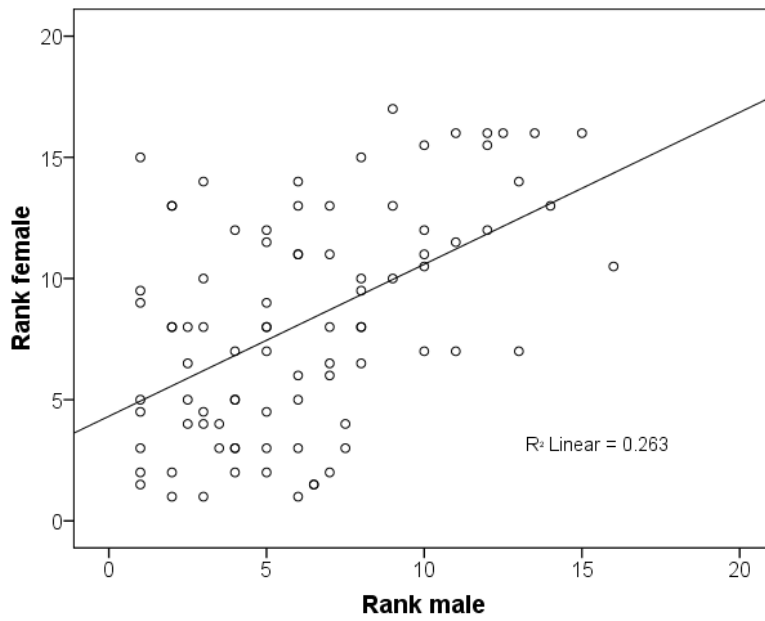Figure 12: Relationship between standard length (SL) of males and females.



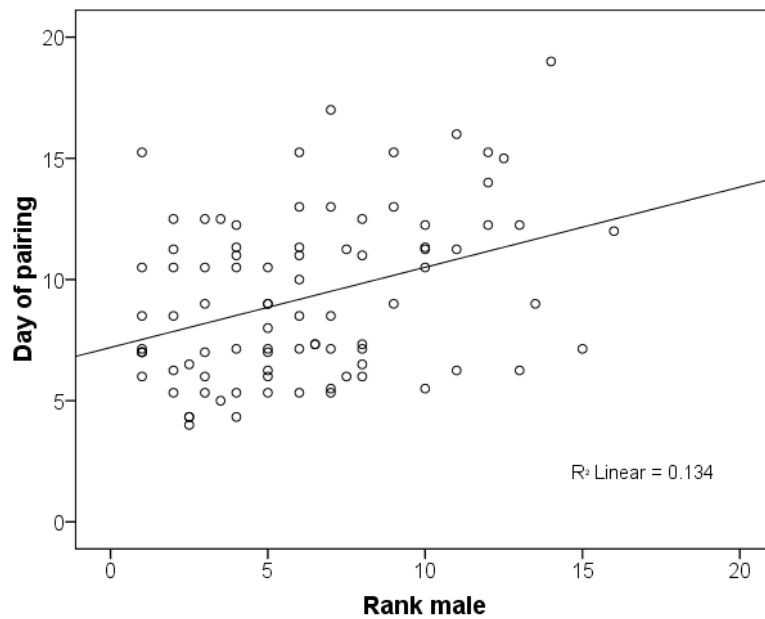Figure 13: Relationship between ranks of individuals in pairs.

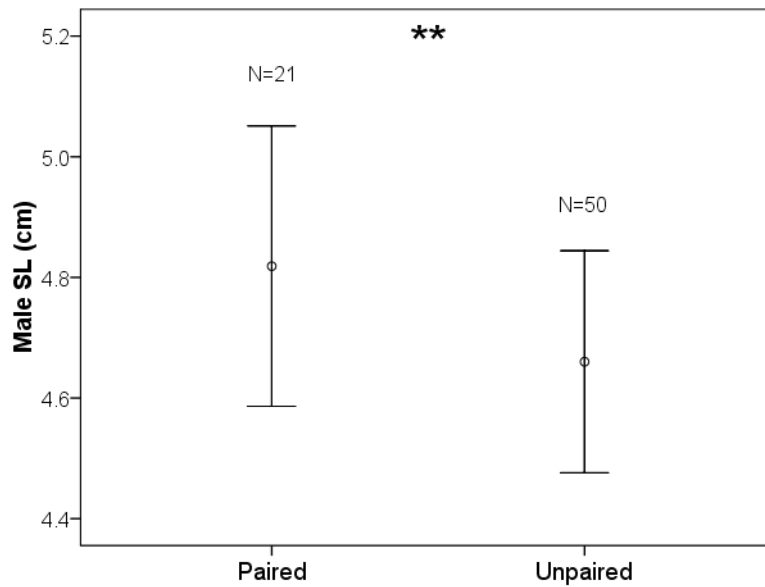Figure 14: Day of pairing in relationship to male rank.



Figure 15: Standard length (SL) of males of the small size class separated in paired and unpaired. Mean ± 1 SD; **: $p < 0.01$.

Pairs mate less assortative in the "Predation" Treatment ($N_1=27$, $N_2=34$, $t=2.080$, $p=0.042$, equal variances; Figure 16). I can exclude that this effect comes from

different fish sizes in the treatments by females (Mann-Whitney U Test: $N_1$=65, $N_2$=80, Z=-0.064, p=0.949; Figure 17) and males (Mann-Whitney U Test: $N_1$=63, $N_2$=80, Z=-0.110, p=0.913; Figure 18). There is no size difference between the females that paired up ($N_1$=27, $N_2$=34, t=1.138, p=0.260, equal variances; Figure 19). According to unpublished field data collected by Schädelin (2007) females are a mean of 82% smaller than their mates.
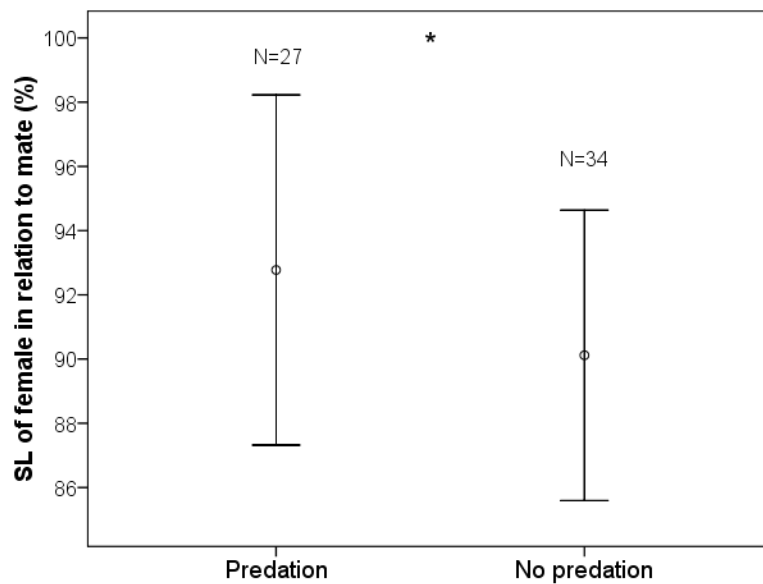


Figure 16: Standard length (SL) of females in relation to their mates in the "Predation" and "No predation" Treatments. Mean ± 1 SD; *: p < 0.05.
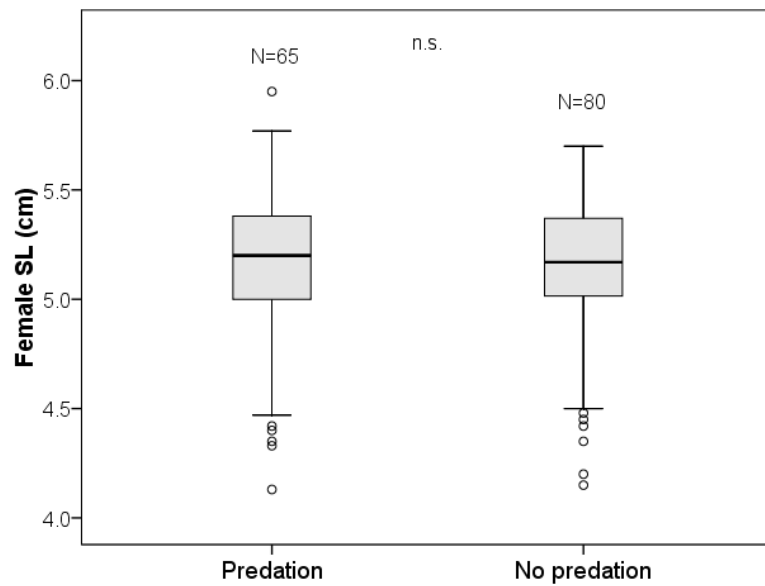
Figure 17: Standard length (SL) of all females used in the experiments. Female sizes between the treatments were similar. Horizontal lines are medians; boxes are upper and lower quartiles, whiskers indicate the highest and lowest values excluding extreme values and outliers. Open circles symbolize moderate outliers (between 1x and 3x interquartile range). n.s.: not significant.
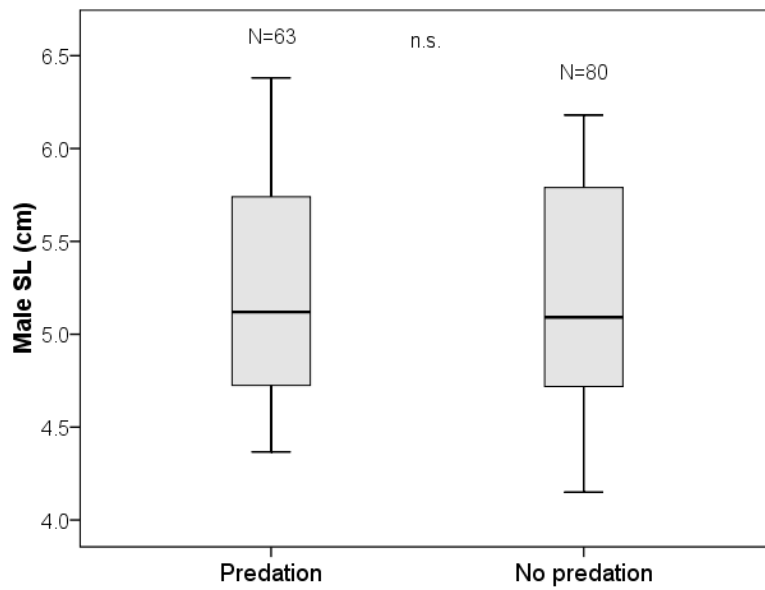
Figure 18: Standard length (SL) of all males used in the experiments. Horizontal lines are medians; boxes are upper and lower quartiles, whiskers indicate the highest and lowest values excluding extreme values and outliers. n.s.: not significant.
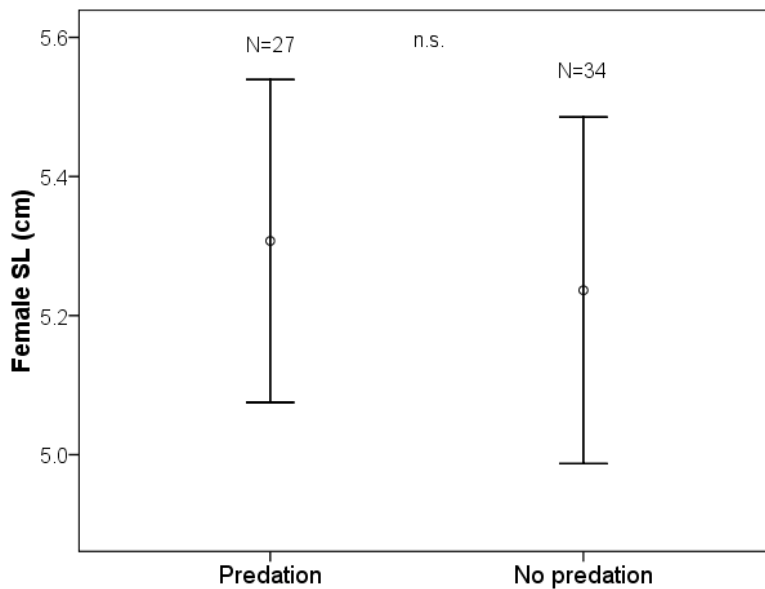


Figure 19: Standard length (SL) of paired females in all experiments until day 12. Mean ± SD; n.s.: not significant.

## 3.5 Polygyny

Predation pressure did not affect the mating system of *N. caudopunctatus* in the experiments (chi$^2$: N=10, p>0.200; Figure 20). The standard length between females paired with monogamous males was similar to the size of females paired first with polygamous males (Mann-Whitney U Test: $N_1$=61, $N_2$=27, Z=-1.226, p=0.220; Figure 21). The size difference between first and second females of a polygamous males is not significant (N=32, Wilcoxon Z=-1.950, p=0.051).
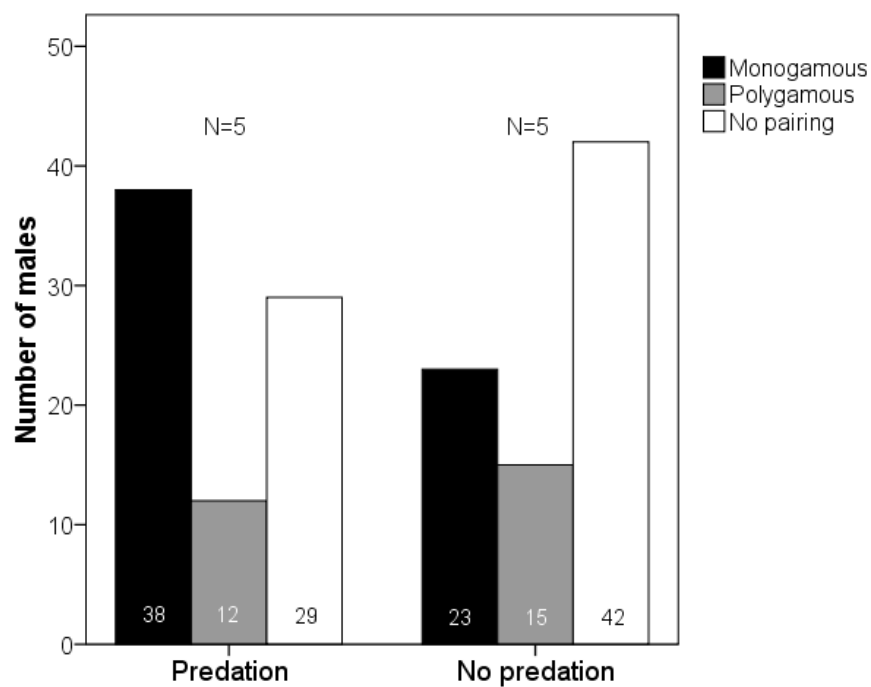


Figure 20: Pairing status of males on day 12 in 5 "Predation"- and 5 "No predation" Treatments of all males in the experiments. The total number of males between the two treatments differs because in one experiment a male was sexed wrong and turned out to be a female.
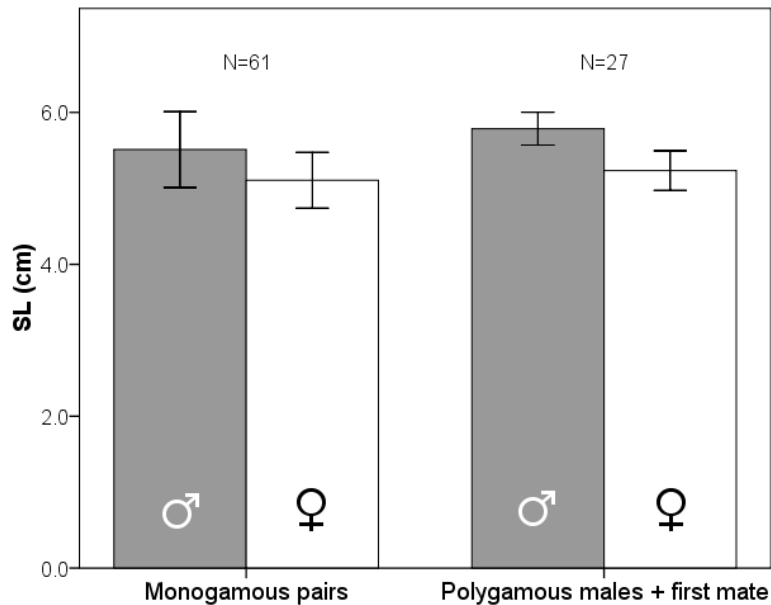
Figure 21: The histogram shows the standard length (SL) of paired monogamous pairs (N=61) and of polygamous males (N=27) and their first mate until day 12 of 10 experimental rounds. Mean ± 1 SD.

Polygamous males did not vary their brood defence behaviour between the clutch of their first or second female. Polygamous males did not attack the presentation tube in front of the breeding cavity of the female they paired with first more often than the presentation tube in front of the breeding cavity of the second female (N=10, Wilcoxon Z=-1.430, p=0.153 (mean ± SD). Male's and female's attack rates compensated each other while defending their breeding cavities (Figure 22). The size of polygamous males ($F_{1,8}$= 0,185; p=0,679), the size of the female ($F_{1,8}$=0,141; p=0,717), the age of the fry ($F_{1,8}$=0,060; p=0,812) and the female attack rate ($F_{1,8}$=2,390; p=0,161) on the presentation tube had no influence on the male attack rate in the double presentations. The size of the female in relation to her mate did not have an effect on the time it took for a polygamous male to pair with a second female (N=29, ρ=-0.149, p=0.441). Whether a female laid eggs did not have an influence on the time it took for a polygamous male to pair with a second mate (Mann-Whitney U Test: $N_1$=19, $N_2$=10, Z=-0.803, p=0.422; Figure 23).
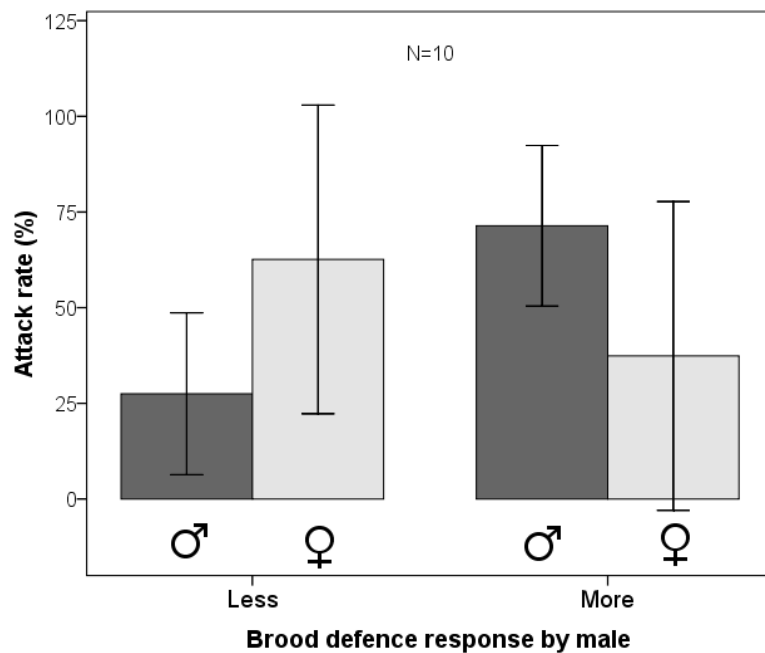
Figure 22: Attack rate on presentation tube at breeding cavity with eggs or fry of polygamous trios. Mean ± 1 SD.
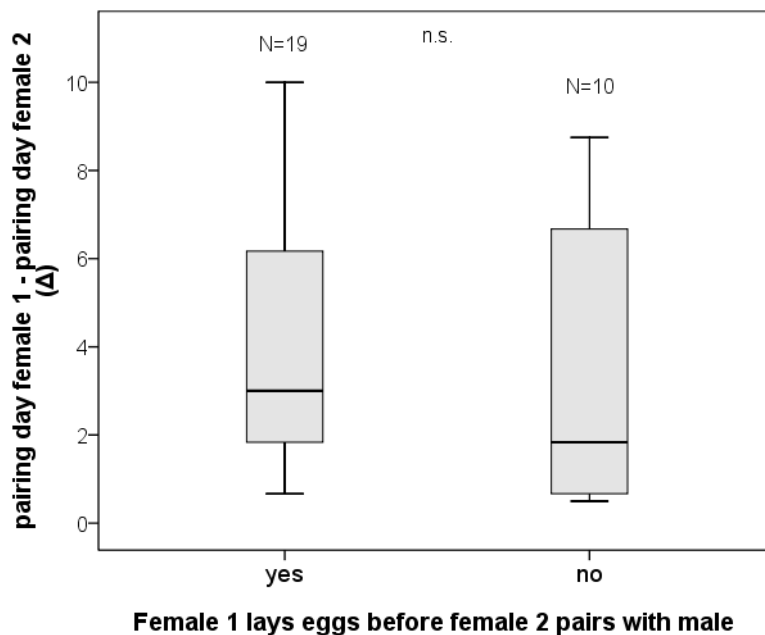


Figure 23: Deviation between pairing of the first female and the day of pairing with the second female of a polygamous male and the influence of the fact that the first female laid eggs or not. Horizontal lines are medians; boxes are upper and lower quartiles, whiskers indicate the highest and lowest values excluding extreme values and outliers. n.s.: not significant.

# 4 Discussion

## 4.1 Colony formation

In this study I was interested in how far predation and sexual selection influence colony formation. I did not find evidence for the hypothesis that colony formation is a by-product of sexual selection, but for the predation hypothesis.

Wagner (1993) suggested that colony formation is a by-product of sexual selection. In a monogamous colonial breeding species females may force their mates to breed near neighbours to obtain extra-pair fertilizations (EPF). If EPF possibilities are low and monogamy limits mate choice, since less mating partners are available, females should switch to better partners within a breeding colony if they have the opportunity. As expected, in the removal experiments I found that it is more likely for large males than small males to get a new mate after being experimentally widowed. This leads to the conclusion that females prefer larger males. However, males did not prefer the largest available females. In most cases new partners were floating females and if not, females who divorced their polygamous partner. Neighbouring females were expected to divorce their partner and trade up to a larger and hence "better" mate. However, being a floater and getting a mate is also an improvement of the mating status and thus considered as a trade up. The same was assumed for a female leaving a polygamous male to pair with a monogamous mate achieving a higher potential level of male parental care and thus trading up. I did not find that floating females are smaller than paired females. This shows that females seem to prefer to wait for a larger mate rather than mate with a small or size-unmatched male. In nature large schools of *N. caudopunctatus* hover above breeding colonies (personal observation), hence the results could lead to an explanation for these phenomena. Reproductively inactive *N. caudopunctatus* wait in-line for a chance to mate. Small floating males were mature (personal observation).

Contrary to the prediction of the Hidden Lek Hypothesis, small males mated faster when they were not near a pair of *N. caudopunctatus* with a larger male. They managed to get a mate faster when they were breeding solitary. Furthermore, first

pairing females did not consequently choose the largest male which suggests, that there must be other traits besides size that influence mate choice. One could also expect that males that breed close to larger males, compromise by waiting longer to breed in order to get a larger female compared to the males that breed earlier and solitarily, but females were similar in size. Under predation pressure, 14 small males were able to get a mate and in absence of predation pressure only 4 small males were able to pair with a female. The reason could be a possible combination of criteria of female choice. One decisive factor could be male size and an additional criterion could be the capability of protecting a breeding cavity from predators by a male ("aggressive performance"). If males could not show their defence abilities in the absence of predators, female mate choice criterion could be limited to male size.

Yet, the results show that *N. caudopunctatus* breeds closer together under increased predation pressure compared to the absence of predators. I considered all breeding cavities for the analysis including the ones of females sharing a mate. Since the frequency of polygamous trios in absence or presence of predators is similar it is not possible that polygyny has an effect on the average neighbour distances.

Behavioural changes in the presence of predators have been shown in many vertebrates (Jennions and Telford 2002; Benard 2004; Walsh et al. 2008). It has been shown that birds and other animals adjust their reproductive investment to the presence of predators, as nest predation plays a key role in reproductive success in birds (Fontaine and Martin 2006) Similarly, breeding pairs invested more in creating a safe cavity for their offspring when exposed to predators. The presence of predators also influenced the readiness of *N. caudopunctatus* to invest in eggs. I found a trend that females lay eggs later when exposed to predation. It remains unclear if females did not lay eggs if they were exposed to predators or if eggs were being predated until the next observation (within 24 h). However, the number of eggs in a brood was not affected by presence or absence of predators. Yet we cannot exclude the possibility that female *N. caudopunctatus* did vary their reproductive investment between the treatments, for example by egg quality. Taborsky et al.

(2007) showed that females of the cooperative breeding cichlid *Neolamprologus pulcher* are able to adjust egg size per brood to the number of conspecific helpers in the breeding cavity.

## 4.2  Mate choice

I found assortative mating by rank and size in the experiment. In the field, females are on average 82% of the male's body size (Schädelin, unpublished data), whereas female size in the experiment was on average 92% of their mates. This difference could be the result of a limited number of possible mating partners. Large males paired earlier than small males. Perhaps large males are more attractive or dominant in competing against other males for females. Looking at the two male size classes separately, I couldn't find a relationship between pairing speed and body size which again might result out of a small variation in body sizes by males.

In the presence of predation pressure, paired females were larger in relation to their mates compared to the absence of predators. The average body sizes of males and females did not vary between the treatments. Maybe males chose bigger females, which might be better defenders. The number of floating females between the treatments did not vary.

In between the small male size class, there seems to be a minimum size to successfully mate with a female, although males are able to reproduce with a standard length of 4 cm (personal observation).

## 4.3  Polygyny

I found polygamous mating males as well as monogamous mating males in the experiment, whereas the species is monogamous in the field. The results provide evidence that a mating system is more the outcome of a reproductive strategy than an evolved characteristic of a species (Bradbury and Vehrencamp 1977). Due to the trade-off between male quality and male parental care females face in polygamous mating (Webster 1991), females should avoid pairing with already mated males in order to increase male parental care especially if high predation pressure induces a high risk of failing to reproduce. In absence of predators, it would not be surprising if

females choose an already mated male in order to pair with a high quality mate. However, predation pressure did not affect the rate of polygamous mating in the experiment. Even if I would double the sample size assuming the same outcome I would not find a significant difference.

Within groups of the obligate coral-dwelling goby, *Paragobiodon xanthosomus* breeding females behaved aggressively towards individuals of their own sex and evicted subordinate females that were large and mature from the group (Wong et al. 2008). In Lapwings (*Vanellus vanellus*) females of polygamous males are smaller in relation to their mate and therefore cannot prevent their mate from getting a second female (Wagner, personal communication). The results do not provide evidence that females can influence the mating status of their mate. Monogamous females of *N. caudopunctatus* and the first females of polygamous males did not differ in size and yet polygamous mating occurred. Furthermore, the time span until the polygamous male gets his second female does not correlate with female size. The fact that the first female laid eggs does also not seem to play a role on the individual mating system. Contrary to the finding of Desjardins et al. (2008), the standard length of polygamous and monogamous males did not differ. Desjardins et al. (2008) found no difference in *N. pulcher* in reproductive success between monogamous and polygamous males, neither did I concerning the clutch sizes. In Red-winged Blackbirds (*Agelaius phoeniceus*) polygyny is influenced by nesting site quality (Pribil and Searcy 2001). The nesting sites in the experiment were all uniform. This could be a reason why I did not find a threshold for polygyny.

Looking at the investment of polygamous males in brood defence I could not find a preference for one of the two females. This is contrary to the finding in some birds that males have a preference for the brood of the first female since older broods (early clutches) already survived a longer period of potential mortality (Willson 1966; Cindy et al. 1980). I found that pairs compensate nest defence effort for their partner. It is unclear whether females compensate attacking for the male or *vice versa*.

Even though I did not find mechanisms that favour polygyny in *N. caudopunctatus* I could show that females show a preference to mate with the largest available mate, whereas males seem to prefer size assortative partners if possible. Furthermore, the results provide evidence that the presence of predators has a direct influence on the reproductive behaviour of *N. caudopunctatus*. Breeding cavities are closer together and the reproductive investment is raised to increase reproductive success.

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# Zusammenfassung

Brutkolonien sind ein weit verbreitetes Phänomen im gesamten Tierreich. Als Brutkolonie bezeichnet man eine dichte Ansammlung von mehreren Brutplätzen, unabhängig vom Futterangebot. Insbesondere bei Vögeln führten Wissenschaftler zahlreiche Studien über koloniebildende Mechanismen durch, obwohl Aggregationen von Brutplätzen auch in vielen anderen Taxa zu beobachten ist, wie zum Beispiel bei Fischen. Ziel meiner Studie ist, zwei Hypothesen zu überprüfen, die Koloniebildung erklären. Die erste Hypothese besagt, dass Tiere Brutkolonien bilden, um den Raubdruck zu verringern. Die Wahrscheinlichkeit dem Angriff eines Räubers zu entgehen ist in einer Gruppe mit Artgenossen größer. Zusätzlich wird die Wachsamkeit gegenüber einem Angriff eines Räubers erhöht. Die zweite zu testende Hypothese ist, ob das Bilden von Brutkolonien nur ein Nebenprodukt von sexueller Selektion darstellt. Die „Hidden Lek" Hypothese besagt, dass in einer monogamen Art die Weibchen ihre unattraktiven Männchen dazu bringen, sich in der Nähe von qualitativ hochwertigeren Männchen („Hotshots") niederzulassen. Man nimmt an, dass Weibchen die Option haben wollen, ihre Partner für einen „Hotshot" zu verlassen, sobald sich die Möglichkeit dazu bietet. Durch dieses individuelle Interesse könnten Kolonien entstehen.

Als Modelorganismus meiner Studie diente der monogame Buntbarsch *Neolamprologus caudopunctatus*. Bei diesem Buntbarsch beteiligen sich beide Elternteile an der Aufzucht des Nachwuchses*. N. caudopunctatus* bildet in seinem natürlichen Lebensraum, dem Tanganjika See, große Brutkolonien. Jedoch sind die Mechanismen, die zu diesen Kolonieformationen führen, nicht erklärt. Das Experiment dieser Studie führte ich in einem ringförmigen Aquarium durch, das nahezu natürliche Bedingung bezüglich der Größe bot. Die potentiellen Bruthöhlen waren gleichmäßig im Becken verteilt. Das Nahrungsangebot war im ganzen Becken gleichmäßig hoch. Zusätzlich beschäftigt sich die Studie mit den Einflüssen auf das Paarungssystem dieser Art, da während der Versuche fakultative Polygamie vorgekommen ist. Diese Beobachtung steht im Gegensatz zu den Erkenntnissen

aus der freien Natur, wo die Tiere sich ausschließlich monogam verpaaren. Generell erwartet man Monogamie, wenn Weibchen weit verteilt sind und Männchen nur ein Weibchen gegen andere männliche Konkurrenten verteidigen können. Auf der anderen Seite wird Polygamie bevorzugt, wenn ein hohes Angebot an Weibchen vorhanden ist und es Männchen möglich ist, mehrere Partnerinnen gegenüber anderen Konkurrenten zu verteidigen. Die Vorteile von Polygamie sind für Männchen offensichtlich, da sie ihren reproduktiven Erfolg steigern, wenn sie sich mit mehreren Weibchen verpaaren. Für ein Weibchen kann es jedoch auch von Vorteil sein, sich auf ein bereits verpaartes Männchen einzulassen, wenn sie dadurch Zugang zu einem qualitativ hochwertigen Partner mit einem qualitativ hochwertigen Territorium erlangen. Trotz alledem sind Weibchen mit einem Konflikt zwischen der Qualität des Männchens und seiner Investition in die Brutpflege konfrontiert.

Obwohl die Resultate keine Antwort auf die Frage nach den Ursachen von fakultativer Polygamie liefern, zeigt sich ein deutlicher Einfluss von Raubdruck auf das Verhalten dieser Cichliden. Der Modelorganismus brütet unter dem Einfluss von Raubdruck näher bei anderen Artgenossen. Zusätzlich verstärkt die Anwesenheit von Räubern das Brutpflegeverhalten. Die „Hidden Lek" Hypothese hingegen scheint für diese Fischart keine Gültigkeit zu haben, da sich kleine Männchen früher verpaaren, wenn sie sich entfernt von größeren Männchen niederlassen. Außerdem verlassen Weibchen ihre Partner nicht wenn sich die Möglichkeit bietet zu einem größeren Männchen zu wechseln. Die „Hidden Lek" Hypothese erwartet in beiden Fällen das Gegenteil.

Die vorliegende Studie ist eine der Wenigen, die experimentell zeigt, dass Raubdruck einen direkten Einfluss auf Koloniebildung hat.

# Acknowledgements

# Curriculum vitae

## Personalia

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## Education

| | |
|---|---|
| 02/2009 – 05/2010 | Diploma thesis at Konrad Lorenz Institute for Ethology, Theme: Colony formation and mate choice behaviour in *Neolamprologus caudopunctatus,* Vienna, Austria |
| 09/2006 – 11/2006 | Field assistant at Lake Tanganyika, University of Bern, Switzerland Topic: Mechanisms of assortative mating in bi-parental mouth brooders |
| 03/2003 –05/2010 | Study of Biology/Zoology, University of Vienna, Austria |
| 11/2001 | Open Water Scuba Instructor (PADI), Grand Cayman, BWI |
| 06/2001 | Abitur at Ricarda Huch-Schule, Gießen, Germany |

## Working Experience

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| 01/2008 – 06/2010 | Zoo Education Department at "Zoo Vienna", Vienna, Austria |
| 11/2009 | Dahab Marine Research Centre, Dahab, Egypt |
| 05/2007 – 10/2008 | Climbing park "Donauinsel", Vienna, Austria |
| 03/2006 – 01/2007 | Konrad Lorenz Institute for Ethology, Vienna, Austria |
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| 07/2004 – 09/2004 | Sinai Blues, Four Seasons Resort, Sharm El-Sheikh, Egypt |
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| 01/2002 – 08/2002 | Camel Dive Club, Sharm El Sheikh, Egypt |
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## Languages

| | | |
|---|---|---|
| German | fluently (oral and written) | mother tongue |
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## Hobbies

Marine life, diving, aquaristik, rock climbing, travelling, soccer