



# Spatial patterns in animal territoriality

Competitive behaviour in a shell dwelling cichlid.

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# Spatial patterns in animal territoriality. Competitive behaviour in a shell dwelling cichlid

*Rumsliga mönster i djurterritorialitet. Konkurrerande beteende hos en snäckskalslevande Ciklid.*

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## Abstract

Sociality among animals is a common phenomenon which has both costs and benefits. More and more studies are published that uses shell dwelling cichlids as a proxy for other taxa because of their convenience when studying, unique evolution and large variety in species. In this study, videos of the species *Neolamprologus Multifasciatus* from Lake Tanganyika has been used to investigate two different questions: 1) If there are any differences between territories of the species on the edge of the larger groups compared to territories in the centre. 2) If *N. multifasciatus* uses sand digging behaviour to gain a competitive advantage against neighbouring territories by depositing sand in the direction of them. This thesis found that there is no significant difference between edge groups and centre groups in the parameters we analysed (aggressive behaviour from the dominant male, time of heterospecific intrusion, digging behaviour of the dominant male, number of group hiding events and time dominant male spends in shell). The thesis also found that *N. multifasciatus* deposits sand in the direction of neighbours more often than would be predicted by chance. We further discuss both our small sample size as well as what our findings means in a broader behavioural context in animals, especially terrestrial animals.

*Keywords:* Behavioural ecology, Edge effect, *Neolamprologus Multifasciatus*, Predation, Territoriality, Territory maintenance

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# Introduction

## 1.1 Sociality in animals

### 1.1.1 Interactions and territories

Social interactions are common in the animal kingdom, from short interactions such as territorial disputes between competing male foxes to lifelong relationships between two mates of swans (Black and Hulme 1996). Both the benefits and costs of living in groups have been well-studied in different taxa (Martinez and Marschall 1999; Booth 1995). However, there are many questions still unanswered such as the evolutionary pressures caused by the social environments on the individuals. These questions remain since the social context is a fluid and dynamic environment where the individual can change the environment itself by, for example, changing social groups (Lein and Jordan 2021). Studying these social interactions can be essential to comprehend which factors decide and creates sociality among individuals and groups. Therefore, conducting research in the field of social behaviour could be significant to give a more profound knowledge of the evolution of these behaviours (ibid).

Territoriality is a common form of social interaction among animals which allows individuals or groups of individuals to control resources within the borders. These territories can be important for both reproduction and survival and thus give an evolutionary edge. Maintaining territory occurs among many different species were a variation of behaviours for defending territory exists. Usually, territories are protected by displays, calls, or scent marking, but defending through “tooth and claws” are not uncommon. According to Powell (2000) resources which restricts population growth creates territorial behaviour within a group or species. One well-studied terrestrial example of territorial behaviour is the red fox *Vulpes vulpes* which is a solitary animal that protects their own territory from competitors to get an advantage in mating success for the males (Giuggioli, Potts, and Harris 2011; Piran and Harris 1994). In rodent’s territorial behaviour is not only seen in males when competing for females but also in females when protecting their young, this at least according to Wolff (1993) which is contradictory to the earlier view that

their territoriality is for food protection. Territories are not only common in individual animals; it also occurs frequently in group living animals such as the red deer *Cervus elaphus*. The stag has been observed to sometimes create territories during the rut to keep their own females away from other stags (Carranza, Fernandez-Llario, and Gomendio 1996). As mentioned, there are many advantages of territoriality but there is an increased cost in other aspects. One example of this is the energy cost of defending a territory, which increases with a higher quality territory, the higher the population density and the more predators there are present. This can lead to injury and a loss of time for both the defending individual as well as the intruding one (Brown 1982).

### 1.1.2 Reducing costs of group living

Even though social group living can lead to an increase in costs for the individual the reward can be greater in group-living organisms. This is in part caused by the spatial positioning of the individual within the group. For example, is the increased competition for food a reason for larger spatial distribution among groups while the increased security from predators a reason for smaller spatial distribution (Couzin et al. 2002; Majolo, de Bortoli Vizioli, and Schino 2008). When considering spatial positioning and its consequences one also has to consider the differences in fitness and costs for different individuals (Krause and Godin 2010). A larger individual might find it more beneficial to be located at the edge of the group to increase its foraging success and will not suffer the same risks from predators as a smaller individual (Krause and Godin 2010; Couzin et al. 2002). Another reason for an outer positioning is for protecting younger and weaker individuals against predation such as bison protecting their calves from wolves by surrounding their young and making a protective wall against the predator (Carbyn and Trottier 1988).

Analogies can be drawn to the selfish herd which is a concept first introduced by W. D. Hamilton in 1971 which states that it is natural for social species to seek shelter in the middle of the surrounding group. This theory states that it is more likely for prey to survive by being close to and in between two others and thus reducing the risk of itself being the individual closest to the predator. Therefore, it is mathematically better for survival to be in the middle than at the edges of the group. This in turn leads to groups tightening further when each individual wants to move into the smaller and smaller gaps between their neighbours (Hamilton 1971). These selfish herds have also been observed as a measure against parasites in some animals and circumstances. Fauchald et al. (2007) showed an example of the benefits of this in reindeer where individuals that lived in herds during the parasite season had fewer warble flies (*Hypoderma Tarandi*) per individual than solitary individuals. This is not always the case as a denser population can sometimes increase the spread of parasites in the population (Arneberg 2001).



## 1.2 Studying cichlids

Fishes have for a long time been relatively unstudied in a cognitive context and the focus has instead been on other taxa's such as primates (Lein and Jordan 2021). More and more studies are coming out with a focus on fishes in general and cichlid fishes specifically (Booth 1995; Bose et al. 2020). Lein and Jordan (2021) argue that shell-dwelling cichlids could be an important part of finding answers to some of the questions in the field of animal behaviour. These questions could be things such as the evolutionary pressure causing sociality and what physiological factors are responsible.

Studying shell-dwelling cichlid, of the genus *Neolamprologus* has been a way to explore the evolution of social and cognitive behaviour. This is, at least in part, caused by the large variation and diversity in social organization and the large number of ecological niches covered by the fishes (Lein and Jordan 2021). These differentiations are present even though many of the species are closely related and recently separated from each other (Pollen et al. 2007). Even though cichlids are possible to study in captivity, such as Budaev, Zworykin, and Mochek (1999) or Bose et al. (2020) problems may arise when sample location and genetic makeup of the test fishes are taken into consideration. For example, did the Bose article use Filial 1 to Filial 3 generations of wild fish and the study by Budaev, Zworykin, and Mochek (1999) uses cichlids from a private breeder. Even though aquariums give a larger control of the experiment they also give a greater uncertainty both in genetic makeup and changes in behaviour between captivity and in the wild. Therefore, observation of wild populations would theoretically be more accurate to the true nature of the fish.

Aggression between the shell-dwelling cichlids have been studied extensively in the last two decades (e. g. Desjardins, Hofmann, and Fernald (2012); Ros, Becker, and Oliveira (2006)) and results show that males are the more aggressive sex. This is the same as in many other species (Cassidy et al. 2017), which suggests that cichlids can be used to model behaviours in many other species with a similar societal composition. Given this background, aggression between neighbouring territories or groups is not a behaviour that is distinct for cichlid species. Similar behaviours have been documented among the wood ant species *Formica aquilonia*, found in the boreal forest (Sorvari and Hakkarainen 2004). Other species that also exhibit traits linked to intraspecific aggression are wolves (*Canis lupus*) (Cassidy et al. 2017). Understanding intraspecific encounters could be essential to expand the knowledge of the advantages of being social for species living in groups, this includes both taxa closely related to cichlids but also taxa that are further removed from them.

### 1.2.1 Shell-dwelling and territory

Some of the smaller cichlids are shell-dwelling and they maintain their territory by moving sand with the help of their mouth or tail. This means that individuals in a group removes sand within the border of their own territory and deposits the sand somewhere else (Gübel, Bose, and Jordan 2021). These territories consist of several empty gastropod shells as well as one dominant male and at least one female but oftentimes there are many non-dominant individuals. These territories have been shown to often consist of closely related individuals (Schradin and Lamprecht 2000). All individuals contribute to the removal of sand from within the territory by either taking mouthfuls of sand and spitting it out somewhere else or by wagging its tail to create currents along the bottom. When there are many females within one territory, they have been shown to create sub-territories that they defend from other females. The females in these territories compete for shells for their own offspring, which means that these shells become the limiting resource in this context. Therefore, fewer shells within a territory the more competition occurs between females (Schradin and Lamprecht 2002). Not only do the females defend their own sub-territories but the dominant male also defends the territory as a whole against conspecifics from neighbouring territories (Gübel, Bose, and Jordan 2021).

## 1.3 Hypothesis

This thesis consists of two different hypotheses. The first hypothesis is that there is a difference between territories that are on the edge and territories in the centre in terms of heterospecific encounters and intraspecific aggression. Our prediction is that there will be a higher cost of living regarding these encounters and aggression on the edge of the larger group than in the centre. The second hypothesis is that *N. Multifasciatus* moves sand in the direction of its closest competitive group as a mean to get a competitive advantage over its neighbours. Our prediction is that this is the case and that *N. multifasciatus* uses sand digging as a mean to maintain territorial borders between territories.

## 1.4 Aim and research questions

The aim of this thesis is to obtain a deeper understanding of animal group behaviour and dynamics. *N. multifasciatus* is used as a proxy for groups at large because of their convenience when studying. They are this for a couple of reasons: The groups, or in this case territories, are easily identifiable, they have a high density of both territories and individuals and live in a largely two-dimensional environment on the lake floor. The questions examined for potential differences examined regarding centre versus edge effects;

- Aggressive behaviour from the dominant male towards both within and without group heterospecific.
- Number of sand-digging behaviour by the dominant male.
- Time spent in the shell by the dominant male.
- Amount of group hiding events, where a group hiding event is defined as at least two individuals within the group hides in their shell.
- Time conspecifics are nearby the territory, both predator species and non-predator species.

The questions examined regarding the sand digging behaviour;

- How often is sand picked up from within/outside the confines of the territory?
- How often is sand deposited within/outside the confines of the territory?
- Is there a non-random directionality to where the sand is deposited?
- Is sand deposited significantly more often in the direction of near-neighbouring territories?

# Method

## 2.1 *Neolamprologus multifasciatus*

The species of cichlid that is studied in this thesis, *Neolamprologus multifasciatus*, is often not larger than 3 cm, shell-dwelling, and lives at the bottom of Lake Tanganyika. They use empty gastropod shells from the *Neothauma* genus as breeding nests and shelter from predators where the female attaches its eggs to the shell wall. These shells make up large fields where territories of *N. multifasciatus* make up groups of territories, where individuals interact with each other and sometimes move between the smaller territories hoping to increase their reproductive success (Schradin and Lamprecht 2002). The emigration is done both by male and female individuals even though females are more likely to do so. These females have been found more likely to move into already occupied territories where they are less likely to receive aggression from the resident dominant male compared to migratory males. However, females are more likely to receive aggression from the resident female compared to the males. The reason for the larger amount of female migration is suspected to be because the migratory females receives protection from the resident male, while migratory males gets no protection from neither resident males nor females (Schradin and Lamprecht 2000).

## 2.2 Field sampling

The data utilised in this thesis consisted of approximately 45 minutes long videotapes displaying social interactions between members in a territory. These videos are taken on the lake floor of Lake Tanganyika, which had a large shell bed on the study site. To map the study area, at a depth of 9-11m, all the territories belonging to *N. multifasciatus* were identified within a study quadrat approximately 10 x 10m. The selected quadrat had a collection of territories isolated from the rest of the shell bed by a border of open sand (appendix 1). A GoPro Hero 7 was positioned facing downward to film video footage of the complete study quadrat to recreate the arrangements of the territories. While filming the GoPro was set to 1080p resolution, 30 fps, and a linear field of view. Within the colony 128

territories, defined as a collection of shells which shelters one dominant male and at least one adult female, were identified. The process of mapping out the territories and filming the videos took place between September and October 2019 (Bose, Koch, et al. 2022; Bose, Dabernig-Heinz, et al. 2022).

Further, to record social interactions among members in a territory several GoPro Hero 7 cameras were used. The cameras were placed in a downfacing position approximately 50cm over the territories and recorded around 50min of film. Out of the 128 territories 22 were selected to be recorded. The settings of the GoPro: s while recording these interactions were the same as when mapping the study quadrant, for analysis only the last 45 minutes were used (Bose P. H 2022).

## 2.3 Video analysis

### 2.3.1 Centre versus edge

Of the 128 territories 20 was used in this study as these territories were deemed to be representative of the whole population. These videos had its focal point in the centre of the group and had a clear picture of the territory and its interactions. The videos were analysed in BORIS v 8.11.1 and a behavioural ethogram was set up (appendix 2). The behaviour of the dominant male was studied according to the ethogram, aggression towards both conspecific and heterospecific individuals was recorded. Digging behaviour and submissive behaviour towards the dominant male as well as heterospecific being nearby was also recorded. The recorded data was then exported to RStudio.

### 2.3.2 Directional spitting

For analysing the spitting behaviour of the cichlids data was collected by mapping the neighbouring territories and subjectively deciding whether spitting behaviour would be categorized as towards the neighbours or not. The videos were analysed in VLC Media player v 3.0.18 Vetinari. Each digging behaviour was recorded by recording the X and Y coordinates for the start and end of the digging behaviour. The coordinates of where the sand was picked up and spat out was recorded, as well as if these positions were inside or outside of the territorial borders.

To map which angular directions were towards neighbours, a person blind to the data estimated the edges of the borders. All spitting behaviours not directed towards these particular angular directions were categorized as not towards neighbours. The percentages of the mapped angular directions were then calculated. If the spitting behaviour is a territorial process the prediction is that more sand is spat towards the neighbours than at the empty borders.

## 2.4 Data analysis

### 2.4.1 Centre versus edge

Of the 20 analysed territories 5 were categorized as edge territories and 15 were categorized as centre territories. Each parameter were quantified by the following:

- 1) The number of aggressive behaviours from the dominant male.
- 2) Number of sand-digging events by the dominant male.
- 3) Time spent in the shell by the dominant male.
- 4) The number of group-hiding events.
- 5) Time heterospecific predators were nearby.
- 6) Time heterospecific non-predators were nearby.

The cost is therefore higher where the amount of aggressive behaviour and amount of heterospecific predators is higher.

Predators and non-predators were categorized by the following:

Predatory species: *Lepidiolamprologus Attenuatus*, *Lepidiolamprologus elongatus* and *Neolamprologus Tetracanthus*

Non-predatory species: *Cyathopharynx Foei*, *Lamprologus Callipterus*, *Limnotilapia Dardennii*, *Neolamprologus Modestus*, *Lobochilotes Labiatus*, *Neolamprologus Cunningtoni* and *Xenotilapia Flavipinnis*.

The research questions were individually analysed. For each parameter a Shapiro and Wilk's test was conducted to check for a normality distribution (SHAPIRO and WILK 1965). Due to the skewness in the data a  $\log_{10}$  transformation for the parameters investigated was conducted to have a normal distribution. With the transformed parameters a linear regression model was conducted. Due to the small amount of aggressive behaviour between the dominant male and adults from other territories only the total amount of aggression showed from the dominant male was analysed, both intra territorial and inter territorial aggression.

The cumulative time of nearby heterospecific, aggression towards conspecific, digging behaviour, time spent in shell and group hiding events parameters were combined into a component principal analysis (PCA) (Jolliffe and Cadima 2016). The PCA was conducted to investigate if there are any correlations between the parameters. This was done in the program JMP-Pro V.16.1.0.

### 2.4.2 Directional spitting

In total 6 territories were analysed, 2 of the territories did not engage in enough digging behaviour during the video trials to be analysed with statistical power. For the statistical analysis a Kolmogorov-Smirnov test (K.S test) was conducted to check for uniformity in the distribution (Feller 1948). This was followed by a probable inference test where the limit values was the end points of the neighbour borders (Wilson 1927). The percentage of spitting events in direction of the neighbours was compared to the percentage of neighbouring border each territory had by a Chi-square test. The significance level was set to  $\alpha = 0,05$  for both analyses.

# Results

## 3.1 Centre versus edge

Only a significance could be found regarding the amount of time the dominant male was hiding in the shells when the two outliers, group 2 and 18, were removed (Est  $\pm$  SE =  $-0,356 \pm 0,164$ , t-value =  $-2,177$ , P =  $0,045$ ).

The following parameters did not have significant difference: Edge groups were not found to be significantly more intruded by heterospecific predators compared to centre groups (Est  $\pm$  SE =  $-0,399 \pm 0,293$ , t-value =  $-1,363$ , P =  $0,19$ ). The same was found for heterospecific non-predator (Est  $\pm$  SE =  $-0,094 \pm 0,290$ , t-value =  $-0,323$ , P =  $0,75$ ) the time for each of these can be found in figure 1 and 2. When combining both non-predatory and predatory intruders there was also no significant difference between edge and centre groups (Est  $\pm$  SE =  $-0,085 \pm 0,263$ , t-value =  $-0,325$ , P =  $0,749$ ).

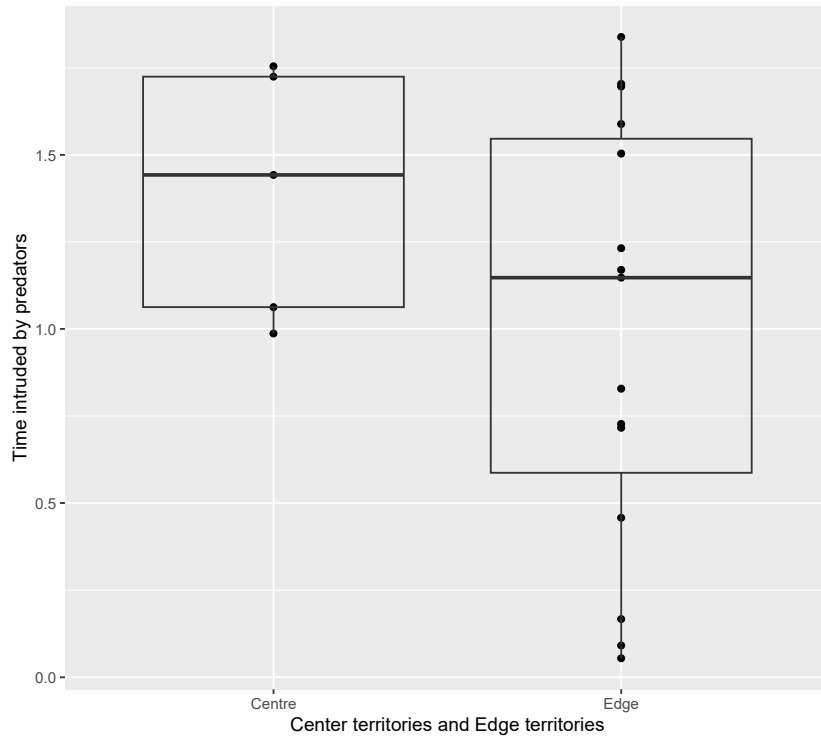
There was also no statistically significant difference found in the amount of group hiding events (Est  $\pm$  SE =  $-0,180 \pm 0,196$ , t-value =  $-0,923$ , P =  $0,368$ ) or the time dominant males were hiding in the shells when the outliers were kept in the analysis (Est  $\pm$  SE =  $0,031 \pm 0,258$ , t-value =  $0,118$ , P =  $0,907$ ).

However, the normal distribution fit poorly for the dominant male's sand digging events with a result on the Shapiro Wilks normality test of P =  $0,065$  and W =  $0,095$  and no significance was found (Est  $\pm$  SE =  $0,742 \pm 0,412$ , t-value =  $1,801$ , P =  $0,089$ ).

No significance could be found regarding the aggressive behaviour from the dominant male towards other conspecific (Est  $\pm$  SE =  $-0,166 \pm 0,257$ , t-value =  $-0,646$ , P =  $0,527$ ).



### intrusion of predators



### intrusion of non predators

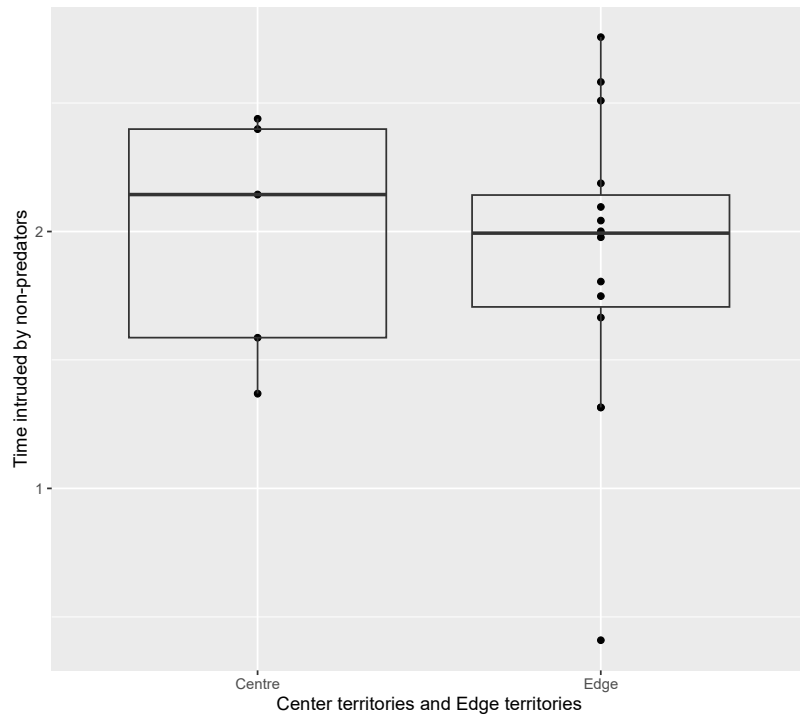


Figure 1: Cumulative time during which groups were intruded upon by heterospecific predators (top) and heterospecific non-predatory (bottom), log-transformed, compared between edge and centre groups of *Neolamprologus multifasciatus*.

The PCA found that Cumulative time intruded by heterospecific, dominant male time spent in shell and number of group hiding events can be grouped together. Dominant male aggression and the dominant male digging behaviour could not be grouped together and point in opposite direction of one another as seen in figure 3 and table 1.

Table 1: Table over the PCA were only the total time of intrusion is included and not predator and non-predator intrusion individually.

Variable	Cluster 1 Coefficients	Cluster 2 Coefficients
Cumulative time intruded by heterospecific	0,651	0
Dominant male aggression Vs another adult	0	0,707
Dominant male time spent in shell	0,585	0
Dominant male number of digging behaviour	0	-0,707
Number of group hiding events	0,484	0

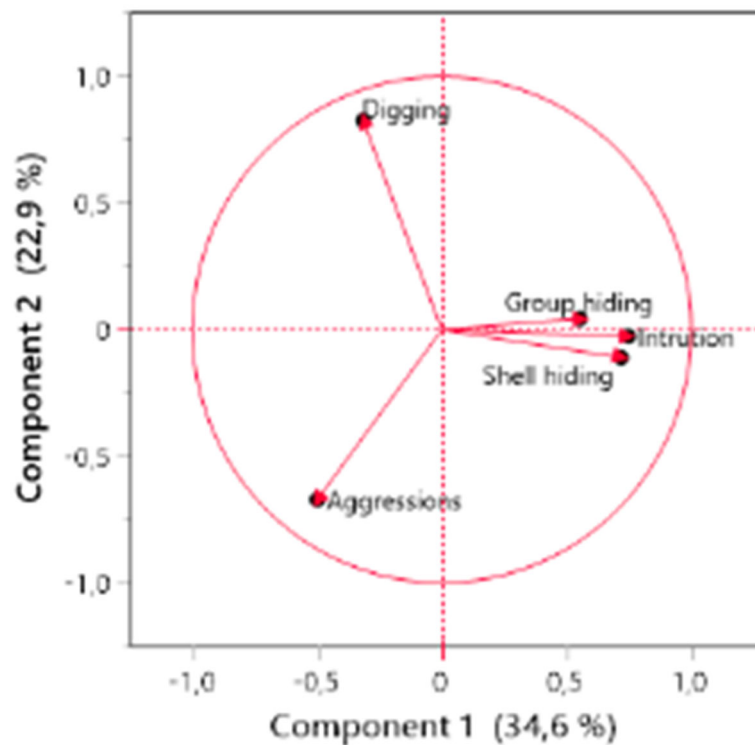


Figure 2: Visualization of the PCA showing a correlation between group hiding, intrusion and shell hiding but these parameters are not correlated to aggression from the dominant male nor digging behaviour by the dominant male.

### 3.2 Directional spitting

The study found that all four studied territories had a directional spitting behaviour with p-value in accordance with table 2 and direction in accordance with figure 3. All territories except group 9 had a significance for directional spitting behaviour towards its neighbouring territories. Sand was most often picked up inside of the territory (750 times) and was most often deposited outside of the territory (865 times). In total was 1039 digging behaviours observed where group 7 had 242 digging behaviours, group 9 had 180 digging behaviours, group 20 had 117 digging behaviours and group 21 had 491 digging behaviours.

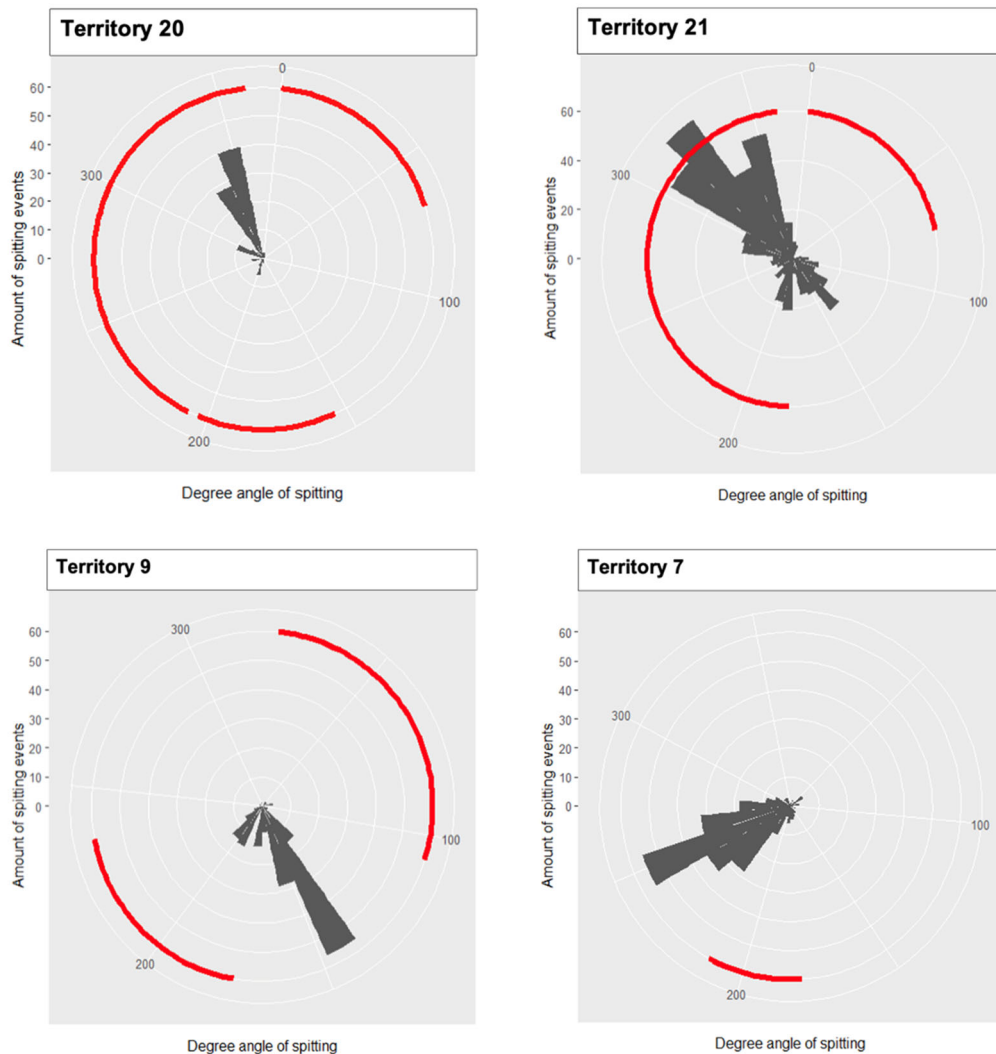


Figure 3: Circular histograms showing the amount and direction of sand spitting. The centre of the graph indicates the centroid of each focal group, and the red lines indicate the directions in which neighbouring groups are located nearby.

Table 2: The result of the analysis regarding spitting behaviour. The P-values states the calculated values for the respective test. Border towards neighbours is the share of border classified as towards nearby neighbours. Spitting behaviour towards neighbours is the share of spitting behaviour classified as towards neighbours.

Group	P-value for the K.S-test	Border towards neighbours	Spitting behaviour towards neighbours	P-value for the Chi-square test
<i>Group 7</i>	< 2,2e-16	0,090	0,256	< 2,2e-16
<i>Group 9</i>	< 2,2e-16	0,405	0,461	0,1442
<i>Group 20</i>	< 2,2e-16	0,897	0,719	2,728e-05
<i>Group 21</i>	< 2,2e-16	0,706	0,831	1,494e-09

## Discussion

Regarding the general idea of the differences between centre and edge group the results were contradictory to what was expected in the hypothesis. This study found that there was a slight overrepresentation of predator species in the centre territories compared to the edge territories. Contrary to the hypothesis, we found no significant effect in any of the parameters analysed between the edge and centre groups.

What was interesting, albeit a bit self-explanatory, was that the PCA found that behaviour and events that was linked to nearby predators and thus danger; group hiding, shell hiding and nearby heterospecific, were linked together. These events were slightly negatively correlated to events that would require there to be no predators nearby, digging behaviour and aggression towards conspecific individuals. This probably means that a group that gets intruded often by predator has less time to both dig and show aggressive behaviour since the group must hide from predators more often. The largest drawback in our study regarding the centre and edge effects was the small overall sample size of only 20 territories as well as the large discrepancy between centre (15 territories) and edge (5 territories). This made it hard to draw any strong conclusions from the analysis which means that our theories were hard to test and our results neither proves nor disproves anything, except that there are no extreme differences between the two categories. It was also hard to find examples of aggression between *N. multifasciatus* from different territories which lead us to compiling all signs of aggression into one parameter including individuals from both the same and different territories.

When considering the environment on the lake floor, the *N. multifasciatus* is limited in its movement and only travels along the bottom of the lake while the predators are not at all limited in depth in the same way. This could mean that the edge effects might be negligible in terms of predation pressure since there are no obstacles for the predators to cross, and they are thus just as likely to prey on centre territories as they are on edge territories. Therefore, other factors might dictate where it is most beneficial to exist, examples of this could be availability of food and migratory patterns of the females. Also, deposition of debris from the water stream might be different at the edge compared to the centre which means that the cost of maintenance is higher at different places within the shell bed. This last point is at

least in part disproven by our study since there was no significant difference in dominant male digging behaviour. However, one would need to compare territories and record all digging behaviour from all resident individuals between groups.

In terms of sand digging the sample size of the number of studied territories was too small to draw any definitive conclusion. The analysed territories were also quite different from one another. Member composition among the territories varied, the smallest consisted of two members and the largest of six members. Further, the level of digging behaviour intensity and how active the cichlids in each territory were, also depended on the group. Some being more active than others which resulted in more digging behaviour, despite in some cases having fewer individuals within the territory. What could clearly be seen from the data was that the spitting behaviour was directional and from our limited data that it was, at least in part, directed against neighbours. One thing that stood out was how most of the fishes seemed to prefer to deposit the sand in a particular direction every time, this direction was unique to each individual in the territory. One idea that struck us when viewing the videos was that this particular direction could be downstream from the territory as this was often the direction that was observed. However, a new statistical analysis of this data needs to be performed to draw any more conclusion.

## Conclusion

The result from this thesis indicates that more territories need to be investigated for both of our research topics. In particular have a more balanced number of edge and centre territories as well as more spitting behaviour from more territories. A comparison from another shell-bed in another part of the lake or another shell-dwelling cichlid could also give a wider understanding on the subject of intra-species competition. By comparing our results with other species, a deeper understanding of cognitive evolution and how cichlids differ from one another could be gained as argued by Lein and Jordan (2021). What was found in this thesis in regard to edge effects was in direct contradiction to some earlier research, for example has an edge effect been found in reindeers in the Fauchald et al. (2007). Our findings were in line with conspecific aggressive behaviours found in the wood ant species *Formica aquilonia* (Sorvari and Hakkarainen 2004). This further supports the ideas that different taxa use different ways to maintain and defend their territories.

## References

- Arneberg, Per. 2001. 'An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence', *Ecography*, 24: 352-58.
- Black, Jeffrey M, and Mark Hulme. 1996. *Partnerships in birds: the study of monogamy: the study of monogamy* (Oxford University Press, UK).
- Booth, David J. 1995. 'Juvenile Groups in a Coral-Reef Damselfish: Density-Dependent Effects on Individual Fitness and Population Demography', *Ecology*, 76: 91-106.
- Bose, A. P. H., J. Windorfer, A. Böhm, F. Ronco, A. Indermaur, W. Salzburger, and A. Jordan. 2020. 'Structural manipulations of a shelter resource reveal underlying preference functions in a shell-dwelling cichlid fish', *Proc Biol Sci*, 287: 20200127.
- Bose P. H, Dabernig-Heinz, Oberkofler, Koch, Grimm, M. Sefc, Jordan. 2022. "Aggression and spatial positioning of kin and non-kin fish in social groups." In *Behavioral Ecology*. Umeå, Sweden: Department of Wildlife, Fish & Environmental Studies, Swedish University of Agricultural Sciences (SLU),.
- Brown, Jerram L. 1982. 'Optimal group size in territorial animals', *Journal of Theoretical Biology*, 95: 793-810.
- Budaev, Sergey V, Dmitry D Zworykin, and Andrei D Mochev. 1999. 'Consistency of individual differences in behaviour of the lion-headed cichlid, *Steatocranus casuarius*', *Behavioural Processes*, 48: 49-55.
- Carbyn, L. N., and T. Trottier. 1988. 'Descriptions of Wolf Attacks on Bison Calves in Wood Buffalo National Park', *ARCTIC*, 41.
- Carranza, Juan, Pedro Fernandez-Llario, and Montserrat Gomendio. 1996. 'Correlates of Territoriality in Rutting Red Deer', *Ethology*, 102: 793-805.
- Cassidy, Kira A., L. David Mech, Daniel R. MacNulty, Daniel R. Stahler, and Douglas W. Smith. 2017. 'Sexually dimorphic aggression indicates male gray wolves specialize in pack defense against conspecific groups', *Behavioural Processes*, 136: 64-72.
- Couzin, Iain D., Jens Krause, Richard James, Graeme D. Ruxton, and Nigel R. Franks. 2002. 'Collective Memory and Spatial Sorting in Animal Groups', *Journal of Theoretical Biology*, 218: 1-11.
- Desjardins, Julie K., Hans A. Hofmann, and Russell D. Fernald. 2012. 'Social Context Influences Aggressive and Courtship Behavior in a Cichlid Fish', *PLoS One*, 7: e32781.
- Fauchald, Per, Rolf Rødven, Bård-Jørgen Bårdsen, Knut Langeland, Torkild Tveraa, Nigel G. Yoccoz, and Rolf A. Ims. 2007. 'Escaping parasitism in



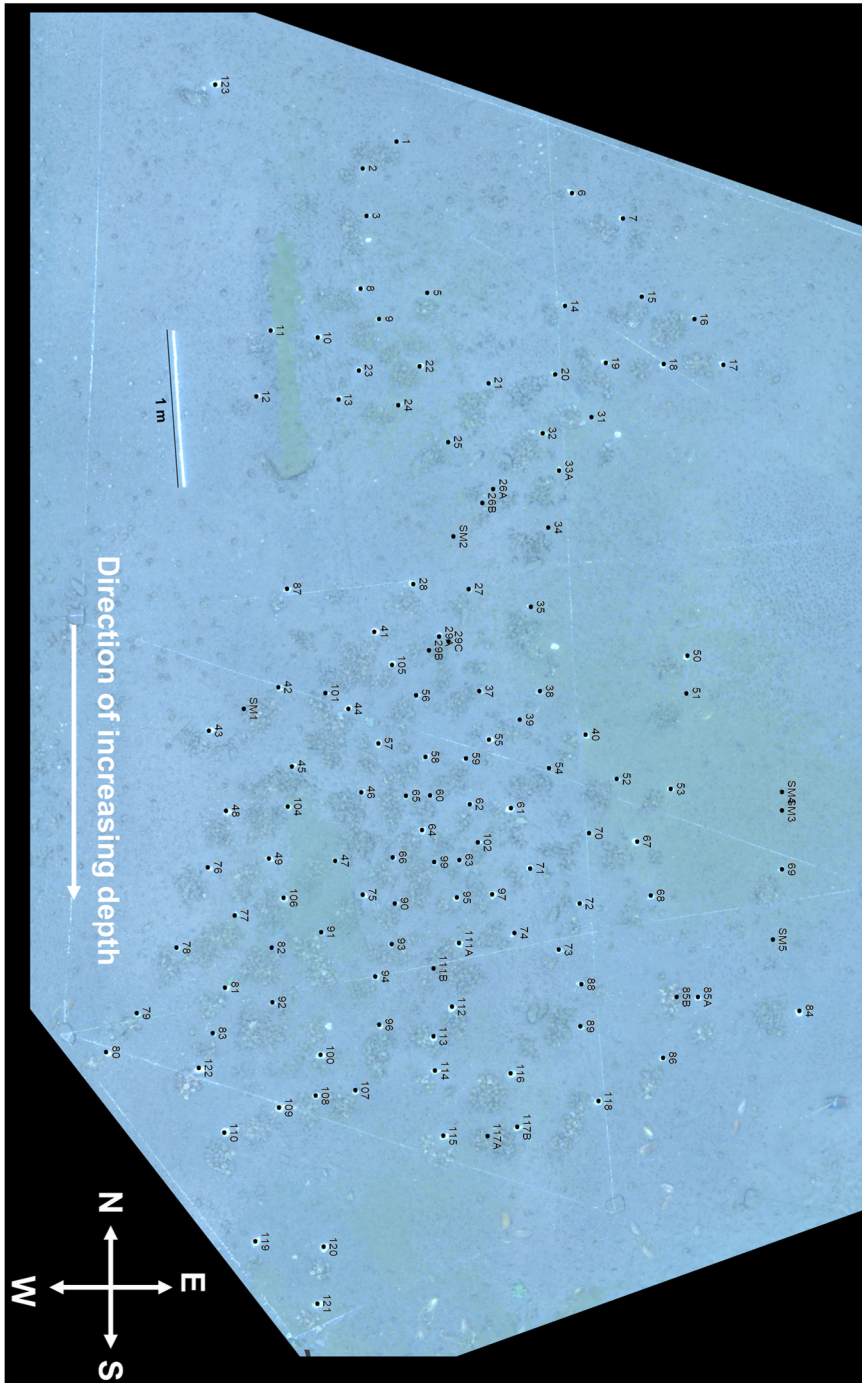
- the selfish herd: age, size and density-dependent warble fly infestation in reindeer', *Oikos*, 116: 491-99.
- Feller, W. 1948. 'On the Kolmogorov-Smirnov Limit Theorems for Empirical Distributions', *The Annals of Mathematical Statistics*, 19: 177-89.
- Giuggioli, Luca, Jonathan R. Potts, and Stephen Harris. 2011. 'Animal Interactions and the Emergence of Territoriality', *PLOS Computational Biology*, 7: e1002008.
- Gübel, Jakob, Aneesh Bose, and Alex Jordan. 2021. 'Social and spatial conflict drive resident aggression toward outsiders in a group-living fish', *Behavioral Ecology*, 32.
- Hamilton, William D. 1971. 'Geometry for the selfish herd', *Journal of Theoretical Biology*, 31: 295-311.
- Jolliffe, Ian T., and Jorge Cadima. 2016. 'Principal component analysis: a review and recent developments', *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 374: 20150202.
- Krause, Jens, and Jean-Guy J. Godin. 2010. 'Shoal Choice in the Banded Killifish (*Fundulus diaphanus*, Teleostei, Cyprinodontidae): Effects of Predation Risk, Fish Size, Species Composition and Size of Shoals', *Ethology*, 98: 128-36.
- Lein, Etienne, and Alex Jordan. 2021. 'Studying the evolution of social behaviour in one of Darwin's Dreamponds: a case for the Lamprologine shell-dwelling cichlids', *Hydrobiologia*, 848: 3699-726.
- Majolo, Bonaventura, Aurora de Bortoli Vizioli, and Gabriele Schino. 2008. 'Costs and benefits of group living in primates: group size effects on behaviour and demography', *Animal Behaviour*, 76: 1235-47.
- Martinez, Felix A., and Elizabeth A. Marschall. 1999. 'A dynamic model of group-size choice in the coral reef fish *Dascyllus albisella*', *Behavioral Ecology*, 10: 572-77.
- Piran, C. L. White, and Stephen Harris. 1994. 'Encounters between Red Foxes (*Vulpes vulpes*): Implications for Territory Maintenance, Social Cohesion and Dispersal', *Journal of Animal Ecology*, 63: 315-27.
- Pollen, A. A., A. P. Dobberfuhl, J. Scace, M. M. Igulu, S. C. Renn, C. A. Shumway, and H. A. Hofmann. 2007. 'Environmental complexity and social organization sculpt the brain in Lake Tanganyikan cichlid fish', *Brain Behav Evol*, 70: 21-39.
- Powell, Roger A. 2000. 'Animal home ranges and territories and home range estimators', *Research techniques in animal ecology: controversies and consequences*, 442: 65-110.
- Ros, A. F., K. Becker, and R. F. Oliveira. 2006. 'Aggressive behaviour and energy metabolism in a cichlid fish, *Oreochromis mossambicus*', *Physiol Behav*, 89: 164-70.
- Schradin, C., and J. Lamprecht. 2000. 'Female-biased immigration and male peace-keeping in groups of the shell-dwelling cichlid fish *Neolamprologus multifasciatus*', *Behavioral Ecology and Sociobiology*, 48: 236-42.
- Schradin, Carsten, and Jürg Lamprecht. 2002. 'Causes of Female Emigration in the Group-Living Cichlid Fish *Neolamprologus multifasciatus*', *Ethology*, 108: 237-48.

- SHAPIRO, S. S., and M. B. WILK. 1965. 'An analysis of variance test for normality (complete samples)†', *Biometrika*, 52: 591-611.
- Sorvari, Jouni, and Harri Hakkarainen. 2004. 'Habitat-related aggressive behaviour between neighbouring colonies of the polydomous wood ant *Formica aquilonia*', *Animal Behaviour*, 67: 151-53.
- Wilson, Edwin B. 1927. 'Probable Inference, the Law of Succession, and Statistical Inference', *Journal of the American Statistical Association*, 22: 209-12.
- Wolff, Jerry O. 1993. 'Why Are Female Small Mammals Territorial?', *Oikos*, 68: 364-70.

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# Appendix 1



## Appendix 2

Behaviour	Description
<b>Aggression</b>	
Frontal display	The focal fish faces another fish and spreads its opercula and pectoral fins. Often associated with forward and backwards movements of the body, and/or a rigid body position.
Lateral display	The focal fish positions its body laterally with another fish and adopts a rigid body. Often accompanied by the focal fish thrashing its caudal fin towards the opponent.
Bite/chase/ram	The focal fish accelerates towards another fish and typically makes contact.
Mouth wrestle	The focal fish locks jaws with another fish and they push against each other.
<b>Submission</b>	
Submissive display	The focal fish positions its body laterally to another fish and shows its belly. Often accompanied by body quivers.
Flee	The focal fish accelerates away from another fish, often entering into an empty gastropod shell for shelter.
<b>Miscellaneous</b>	
Shell hiding	The focal fish hides in an empty gastropod shell for a duration of time.
Group hiding	Some or all the fish in the group dive into their shells.
Sand digging (mouth)	The focal fish takes a mouthful of sand or debris and spits it out elsewhere.
Sand digging (tail)	The focal fish moves sand and debris forcefully by beating its tail at a high frequency against the ground. This action drives the sand away behind from them.
Heterospecific nearby	This is when other species are within the camera's field of view. Identify them down to species in the modifier column.

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