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ADVANCES IN CICHLID RESEARCH VI

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The role of neighbours in aggressive defence of territories in mixed-species breeding aggregations of cichlid fish

Topi K. Lehtonen · Heikki Helanterä

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Abstract While territorial aggression is a prerequisite for reproduction in many animals, individuals need to balance its benefits against the costs. Territorial neighbours can influence these costs and benefits, yet their role is often poorly understood, especially in neighbourhoods with heterospecifics. To address this topic, we assessed both the overall (i.e. neighbourhood-level) and species-level aggression towards an intruder in naturally formed mixed-species neighbourhoods of Nicaraguan cichlid fish. We found that while the territories were tightly packed and territory holders were likely to benefit from neighbours that are aggressive towards intruders, the burden of intruder repellence fell mainly to the territory owners closest to the intruder. Moreover, the overall aggression did not markedly increase with the number of territories, further indicating that the investment by most territory holders decreased with territory density. While some species appeared better neighbours than others in terms of their contribution to the neighbourhood-level defensive aggression, the patterns of species co-occurrence did not reveal significant species pair-specific associations. Overall, these results are consistent with the selfish herd theory and suggest that territory defence against intruders can impact the composition of the local community.

Keywords Aggression bias · Behaviour · Community ecology · Dear enemy · Group dynamic · Mobbing

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T. K. Lehtonen (✉)
Natural Resources Institute Finland, Paavo Havaksen Tie 3, 90570 Oulu, Finland
e-mail: topi.lehtonen@luke.fi

H. Helanterä
Ecology and Genetics Research Unit, University of Oulu, PO Box 3000, 90014 Oulu, Finland

Introduction

In many animals, success in reproduction or foraging requires aggressive defence of a territory. However, such territorial aggression is typically costly due to, for example, energy expenditure, risk of injury, risk of predation or time allocation away from other key activities (Riechert, 1988; Marler & Moore, 1989; Jakobsson et al., 1995; Neat et al., 1998; Briffa & Sneddon, 2007). Especially when intruders pose a risk of predating on the territory holders or their offspring, having territorial neighbours may alleviate the costs. For instance, predators may, on average, have a lower success when harassed by multiple neighbours, each of which is defending a nest or territory (Robinson, 1985; Wiklund & Andersson, 1994; Krams et al., 2009). In addition, the predator may leave the area quicker when it is attacked with a sufficient intensity that is more easily reached with a larger number of participating individuals. Aggression towards an intruder by multiple neighbours can be cooperative, in which case it is often called mobbing (birds: Curio, 1978; Cunha et al., 2017; Dutour et al., 2019; mammals, fish and invertebrates: Carlson et al., 2018; Carlson & Griesser, 2022), while territorial aggression by neighbours can provide safety even when it is not preformed cooperatively. In this context, intruders are often thought to be nest predators, while non-predatory territorial challengers, such as competitors over mates or resources, can similarly pose a frequent threat and be evicted by multiple neighbours (Elfström, 1997; Detto et al., 2010).

Heterospecific neighbours may provide territory defence benefits in similar ways to conspecifics, while presumably being less significant sexual and resource competitors. This is relevant because mixed-species groups are a prominent type of social organisation in many habitats and animal taxa (Terborgh, 1990; Stensland et al., 2003; Paijmans et al., 2019). Moreover, mixed-species neighbourhoods may contain a wider variety of sensory abilities that help with general intruder detection, or certain resident species may be particularly effective towards specific intruders of high threat (Burger, 1984; Semeniuk & Dill, 2006). Such potentially beneficial associations may take place between relatively equal residents (Kleindorfer et al., 2009; Ibáñez-Álamo et al., 2015) or a smaller species may exploit aggression of bolder and more aggressive ones to gain protection against nest predators and other intruders (Haemig, 2001; Quinn & Ueta, 2008).

In both single- and mixed-species neighbourhoods, the costs versus benefits of neighbours are likely to result in complicated trade-offs. Benefits of having many neighbours (a high territory density) are likely to include increased vigilance and quicker or more efficient intruder harassment (Elfström,1997; Quinn & Ueta, 2008; Detto et al., 2010), while potential costs include aggression and competitive interactions (Dunn et al., 2015), predator attraction (Frauendorf et al., 2022) and parasite transmission (Godfrey et al., 2010). Local territory density is likely to depend on the balance between such costs and benefits, which may accrue not only from the neighbour density per se but also from the neighbours' characteristics. In other words, variation in local territory density may be driven by neighbourhood-specific effects. However, the drivers of such multi-species territory neighbourhoods are not well understood.

In fish, mixed-species associations are common for instance in coral reefs and species rich freshwaters (Talbot et al., 1978; Paijmans et al., 2019). In Lake Xiloá, a Nicaraguan crater lake, more than 10 cichlid (Cichlidae) species in 8 genera have highly overlapping breeding seasons, during which they aggressively defend territories from both conspecifics and heterospecifics that pose a risk of taking over the territory, predating on their offspring or both (McKaye, 1977a). The territories are established on the lake floor for the purpose of reproduction and are defended typically, but not exclusively, in a biparental fashion until the juveniles are ready to disperse at the age of a few weeks (Lehtonen et al., 2011a,b). Earlier studies suggest that, in such cichlid fish aggregations, not all neighbours or intruders are equal (McKaye, 1977b; Lehtonen et al., 2015a,b; Lehtonen, 2019; Santangelo et al., 2024). Costly neighbour interactions (Lehtonen & Lindström, 2008; Lehtonen et al., 2015b; Santangelo et al., 2024) aside, some neighbours potentially provide benefits in terms of reduced offspring predation or energy expenditure (McKaye, 1977b; Lehtonen, 2008, 2019). In the mixed-species settings, an intruder is sometimes harassed by multiple individuals and species until it flees or succeeds in its intrusion (Lehtonen, personal observations 2005–2016). In such situations, cooperation might increase efficacy of territorial defence.

Thus far, neighbourhood dynamics in Lake Xiloá and elsewhere have mostly been assessed between conspecifics or specific species pairs. However, when multiple species share the same breeding grounds, a better understanding of the roles of different neighbours may require an approach that includes all relevant members of naturally formed neighbourhoods. Accordingly, our objective was to assess the aggression by all territory holders of natural mixed-species neighbourhoods in relation to territory (i.e. neighbour) density and species composition. To do this, we investigated, using Lake Xiloá cichlids, whether neighbourhood-level aggression towards an intruder correlates with territory density (i.e. the local number of aggressors), which would indicate active participation of neighbours to the burden of territory defence. Lack of a density effect in aggression would, in turn, suggest that territory holders use, on average, less energy in higher territory densities. Here, we also assessed how aggression relates to the intruder's proximity. The array of territorial species in the neighbourhood may also be relevant, and we, therefore, tested whether specific species drive the neighbourhood's overall rate of defensive aggression, either by being aggressive, affecting the aggression of their neighbours or both. In this respect, species might differ in their willingness or ability to react to intruders, potentially affecting their neighbours' territory defence and hence their own desirability as neighbours (birds: Haemig, 2001; Quinn & Ueta, 2008; these cichlids: McKaye, 1977a,b; Lehtonen, 2008, 2019). We also expected that if particularly well (or badly) functioning species pairs shape formation of the neighbourhoods, the occurrence of specific pairs of species in the neighbourhoods would be non-random.

Methods

The study was set up in November, and it was completed in December 2016, in Lake Xiloá, Nicaragua (12°12.8' N; 86°19.0' W). Lake Xiloá is a relatively small (~4 km^2) and deep (average depth: 60 m) crater lake with interesting fish fauna that includes endemic cichlid species (McKaye, 1977a; Elmer et al., 2009). The study coincided with high breeding activity (i.e. many active breeding territories) by most of the cichlid species in the lake (Lehtonen, personal observations 2005–2016). During the study period, the water was relatively clear with 3–5 m of vertical visibility.

To assess the species co-occurrence and neighbourhood patterns of territorial aggression in natural neighbourhoods, we first defined the exact points where the replicates of the experiment, hereon referred to as 'trials', were later conducted. This was done haphazardly with regard to the cichlid neighbourhoods, as follows. We sought a general area that was earlier identified as one of the main cichlid breeding sites in the southern part of the lake, as judged by the range of species and density of territories on the lake floor. The habitat consisted of a mix of stones, pebbles, sand and organic matter. After arriving to the site, a diver dropped a small, numbered piece of ceramic tile to the lake floor at a depth of 12 m. The diver then followed the 12 m depth contour (as assessed by a dive computer) and dropped similar markers with a minimum distance of 2 m between any two markers, forming a line of 18 markers that was roughly parallel to the shore. The diver then swam towards the shore for slightly over 2 m and started to swim in parallel to the original line, dropping markers so that the minimum distance between any two markers was always 2 m. In total, we established 6 parallel lines of 18 markers that formed a 6 × 18 grid of markers on the lake floor. One trial was later conducted on each point of the grid, as detailed below.

We ran the trials 7–17 days after the grid had been completed. The assessment order of the 108 grid points was randomised, so that no adjacent points were assessed during the same day (to minimise recent disturbance). Hence, the trials were as random as possible with regard to the composition of the neighbourhoods, as well as sources of noise, such as the phase of the reproductive cycle. We ran one trial at each grid point, with 3–15 trials run per day. At the start of a trial ($N = 108$), a diver approached the assigned grid point, being careful to minimise the disturbance to any territories in the vicinity. First, the diver recorded the territory holder species and the approximate location of the centre of each territory within a 1 m radius from the focal grid point. The 1 m distance corresponds with earlier observations of the typical maximum distance from which territory holders may react aggressively to intruders (Lehtonen et al., 2011b; Lehtonen, personal observations 2005–2016). The location of the centre of the territory was estimated by the behaviour of the territory holders; it was where the territory holders spent most of their time and where, when visible, the school of fry was typically centred (Lehtonen et al., 2011b). The diver checked and calibrated the distance estimates multiple times and found them to have a good accuracy (± 10%).

Two minutes later, the diver initiated the aggression assessment by placing an intruder dummy (see below for details) on the pre-existing grid point and then backed off to a direction that minimised the overall disturbance. The diver then counted the number of aggressive responses by any fish towards the intruder dummy for 5 min (noting the species of the aggressor). Here, all territory holders were similarly behaving cichlids and most species were of similar size, allowing us to pool their aggressive responses when assessing the neighbourhood-level aggression. In addition, species identities were accounted for in the statistical analyses (see below). Aggressive responses by all species involved either a rapid advance–typically followed by a bite and retreat back to the centre of the territory–or a slow glide towards the dummy with pronouncedly flared gill covers (opercula) and fins, together corresponding to the 'total aggression rate' of earlier studies (e.g. Lehtonen et al., 2015a,b; Oldfield et al., 2015).

To emulate typical territorial intrusions in this community, we chose to use a single dummy of the black devil (*Amphilophus sagittae*) dark colour morph in all trials. This species is particularly common in the area, and both a potential breeding territory competitor to, and offspring predator of, other cichlid species that share the same breeding grounds (Lehtonen et al., 2015b; Lehtonen, 2019). The same dual role is also true for most other members in this community. Following Lehtonen et al. (2015a,b), we constructed the intruder dummy by glueing waterproof, photographic colour prints of a digital photo of the lateral side of a black devil (dark colour morph, unknown sex) onto both lateral sides of an oval shaped polypropylene plate (thickness: 6 mm). The length of the dummy, 16 cm, corresponded to a relatively small adult black devil (Lehtonen, 2014). It was attached to a sinker with a 15 cm long fishing line, allowing it to float in a natural position above the lake floor. Such intruder dummies (with photographic or artificial colours) allow quantification of aggression and have been successfully used in a wide array of studies on birds (Syrová et al., 2016; Tryjanowski et al., 2018) and fish (Rowland, 1999), including aggression assessments in a range of Neotropical cichlids (Cravchik & Pazo, 1990; Barlow & Siri, 1994; Beeching, 1995; Lehtonen et al., 2015b, 2016; Anderson et al., 2016).

To assess the role of key species in the patterns of overall, neighbourhood-level aggression, we narrowed our formal investigations to the four most common species in the area: the black devil, moga (*Hypsophrys nicaraguensis*), poor man's tropheus (*Neetroplus nematopus*) (also known as *Hypsophrys nematopus*) and red breast cichlid (*Cribroheros longimanus*). The territories of these species constituted over 97% (279/286) of all territories recorded in the trials of the current study. In 8 of the 108 trials, no cichlid territories were present within the 1 m radius and they were, therefore, excluded from the statistical analyses.

Statistical analyses

We used R 4.2.2 software (R Core Team 2022) for all analyses. To address the patterns of neighbourhood-level aggression directed towards the intruder, we applied generalized linear models (GLMs) with a negative binomial distribution ('glm.nb' function in R), as appropriate (Zuur et al., 2013) for overdispersed (as assessed by the 'check_overdispersion' command) count data. In particular, our response variable of interest was the total number of aggressive responses towards the intruder dummy. To assess the importance of the identity of the species present in the neighbourhood, and the robustness of the other effects (see below) in relation to species differences, we applied an information-theoretic (IT) framework (Garamszegi, 2011). Here, instead of interfering from just a single model, we included the presence of the above four species in all possible combinations. Each model included the presence (yes/no) of 0–4 cichlid species and we fitted a model for each of the 16 possible species combinations. To address the effect of the number of territories (i.e. neighbours), all 16 models also included the number of territories within the 1 m radius from the intruder dummy as another response variable. All 16 models also included the distance between the dummy and the nearest cichlid territory as an explanatory variable to account for this effect. We used the Akaike information criterion (AIC) to order these models in terms of their fit. We then drew interpretations of the relative performance of the 16 models.

To further assess the role of the territory closest to the intruder, the distance to the intruder, and territory holder species, we assessed species-level aggressions with a generalized linear mixed model (GLMM) with a negative binomial distribution ('glmmTMB' function in R). Here, the response variable was the species-specific number of aggressive responses per trial. The explanatory variables were the identity of the species, whether that species was the closest to the intruder (yes/no), the closest distance of any territory of that species to the intruder (in cm) and the number of territories of that species in the neighbourhood (i.e. trial). Note that if the distance approximations of two (or more) species were the same, both species were conservatively denoted as not being the closest one. Results regarding this effect would be similar, but more pronounced, if both were designated as being the closest. Because many neighbourhoods had more than one species, we added trial identity (i.e. grid point ID) as a random effect.

Finally, to further understand the composition of the neighbourhoods, especially regarding whether certain species occur disproportionately often (or rarely) together, we carried out hypergeometric tests on the pairwise co-occurrences of each species pair. This was done with the'*phyper*' function and the tests were conducted separately for excess and deficit co-occurrence.

Results

The most commonly encountered species was the moga, followed by the black devil, red breast cichlid and poor man's tropheus (Figs. 1, 2).

All 16 models (Table 1) that addressed neighbourhood-level aggression towards the intruder dummy consistently showed that the distance between the dummy and the nearest territory was important: the overall rate of aggression was higher when the distance was shorter (GLM, $|z| \geq 6.96$, $P < 0.0001$) (Fig. 3a). Interestingly, the number of territories within the 1 m radius from the intruder dummy (i.e. 'density') did not have a significant effect on neighbourhood-level aggression in any of the 16 models (GLM, $|z| \leq 1.599$, $P \geq 0.11$) (Fig. 3b). Indeed, both effects were similar in all models, independent of the combination of species included. We used the full model with all four species for illustrating the two effects (Fig. 3a,b; Table 2). Regarding the four most common species, the moga was particularly important in the sense that it was included in most of the models with the best fit (Tables 1, 2).

Our species-specific analysis confirmed that the distance between the dummy and the territory was the main driver of aggression (GLMM, $\beta \pm SE = -0.05205 \pm 0.00504$, $z = -10.34$, $P < 0.0001$) (Fig. 3c). For a given distance, the rate of aggression was higher when the focal species was the closest one to the intruder than when it was not (GLMM, $\beta \pm SE = 0.5404 \pm 0.2207$, $z = 2.449$, $P = 0.014$) (Fig. 3d). The two most aggressive species were the poor man's tropheus and moga (Fig. 1).

Finally, none of the pairwise co-occurrence patterns deviated from random expectations after a false discovery rate correction (hypergeometric tests, adjusted comparisons, $P > 0.24$) (Fig. 2).

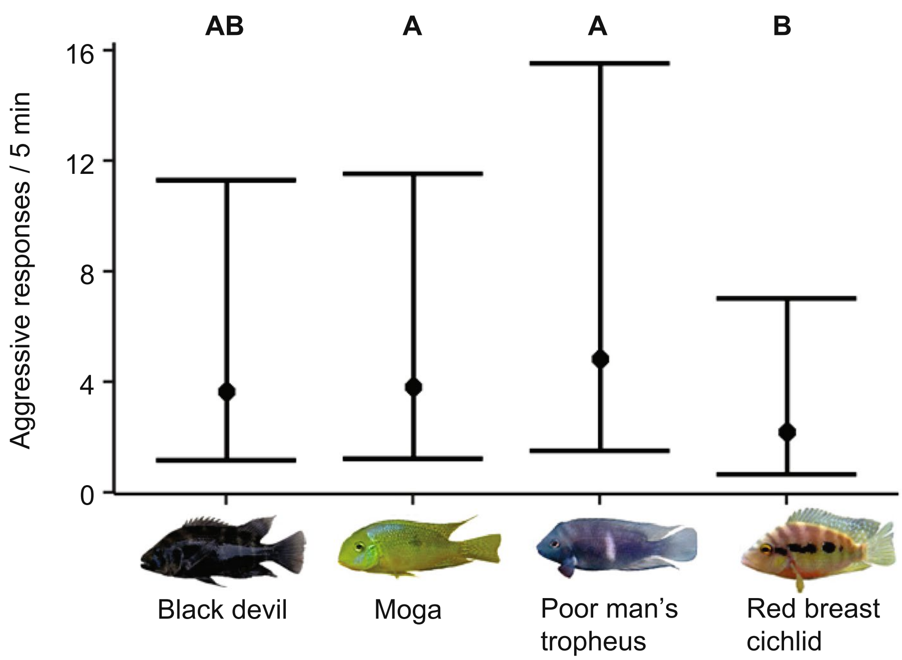

Fig. 1 Species-level aggression effects (GLMM-generated, with 95% confidence intervals) by the four cichlid species most often encountered during the experiment. Species without a letter in common were significantly different ($\alpha = 0.05$). Photos: © Topi K. Lehtonen

Fig. 2 A Venn diagram demonstrating the observed total numbers of territories by species (in brackets) and the number of times the species co-occurred with each other in the neighbourhoods we assessed

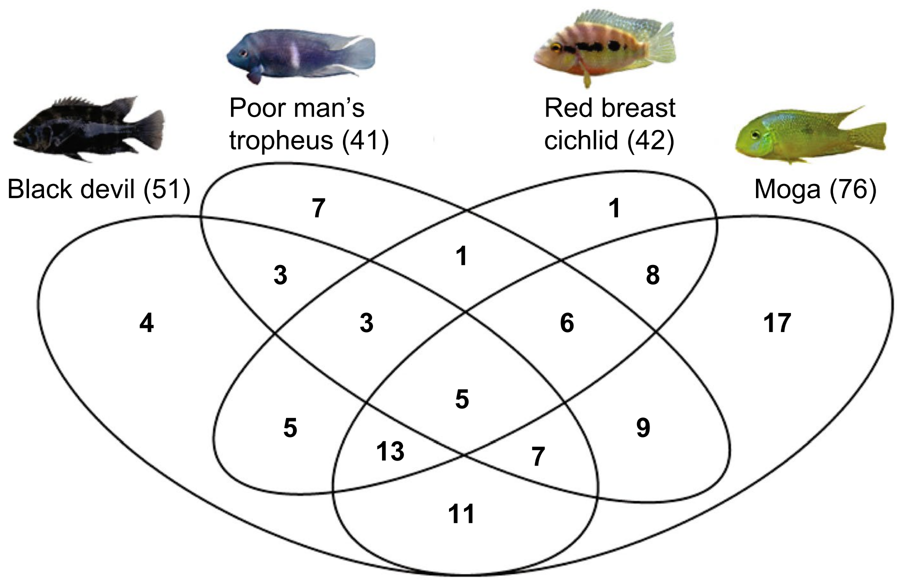

Table 1 Sixteen different negative binomial GLMs on the number of aggressive responses, ranked according to their AIC values, with the model of the best fit ranked as 1

Rank	Species included	df	Δ AIC
1	Moga, poor, red breast	94	
2	Moga	96	1.13
3	Moga, poor	95	1.34
4	Moga, red breast	95	2.00
5	Black, moga, poor, red breast	93	2.00
6	Black, moga	95	2.94
7	Black, poor, red breast	94	3.31
8	None	97	3.46
9	Black, moga, red breast	94	3.78
10	Red breast	96	3.88
11	Black	96	3.90
12	Black, red breast	95	4.34
13	Poor, red breast	95	4.37
14	Black, poor, red breast	94	4.96
15	Poor	96	5.14
16	Black, poor	96	5.63

Black black devil (*Amphilophus sagittae*), *moga* moga (*Hypsophrys nicaraguensis*), *poor* poor man's tropheus (*Neetroplus nematopus*), *red breast* red breast cichlid (*Cribroheros longimanus*)

Discussion

The (arbitrarily defined) neighbourhoods assessed in this study often had multiple territories in close proximity (more than 1 territory in 81/100 of the neighbourhoods, maximum number of territories: 7). However, aggression towards the intruder dummy did not significantly increase with the number of territories. Therefore, it seems unlikely that cooperative defence would drive territory densities, and, instead, other factors are likely to play a larger role. The result also implies that the costs of territory defence, in terms of the number of aggressive responses per each breeding pair (/individual), decreased with the territory density. However, the current study did not address to which extent a more densely packed neighbourhood might lure higher numbers of intruders. In this respect, while intruders aspiring to predate on offspring might be attracted by a high territory density, we expect new territorial challengers, in contrast, to be discouraged by higher densities of territory defenders.

The results show that the intruder's distance to the nearest territory is a very important predictor of the overall aggression subjected to it. Combined with the lack of an effect of number of territories on the neighbourhood-level aggression, this finding suggests that territory densities are shaped by the so-called selfish herd effect, in which aggregations are formed by each individual (here: pair) trying to minimise its 'domain

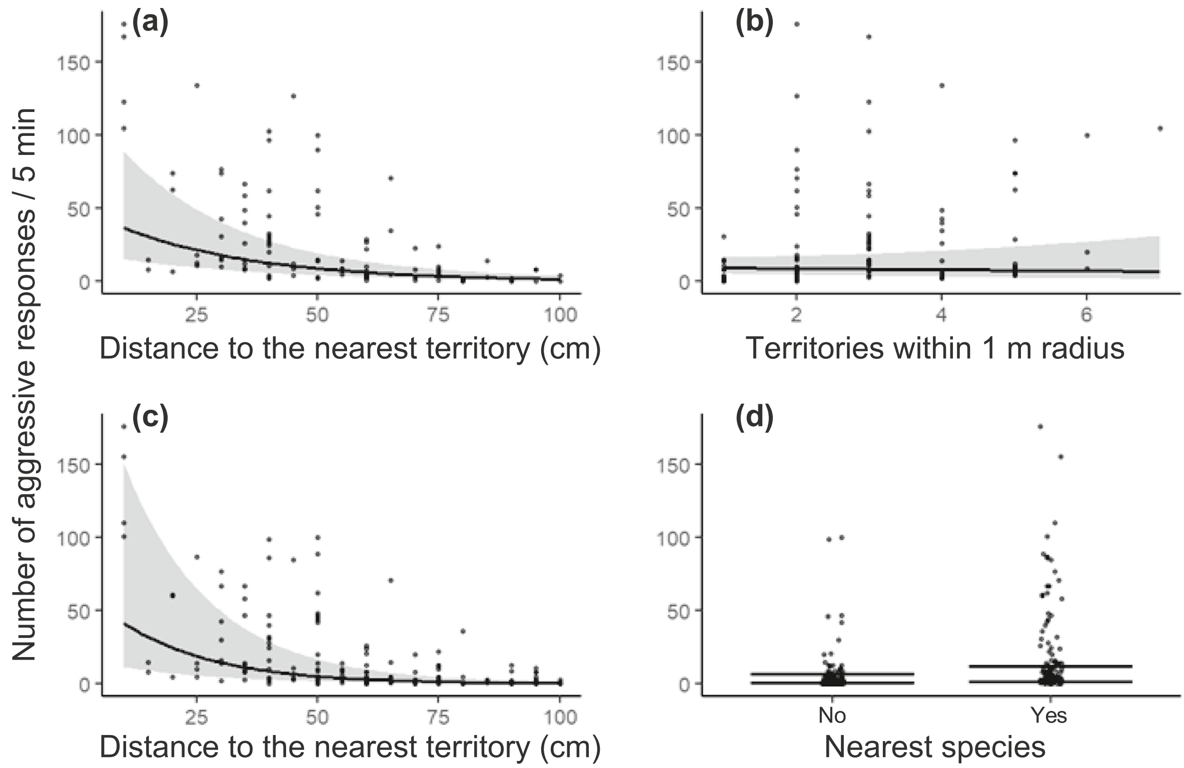

Fig. 3 Model-generated predictions and non-adjusted datapoints for (a) neighbourhood-level aggression in relation to the distance between the nearest territory and intruder dummy, (b) neighbourhood-level aggression in relation to the number of territories within 1 m radius from the intruder, (c) species-level aggression (the number of aggressive responses per species per trial) in relation to the distance between the nearest territory and intruder dummy and (d) species-level aggression in relation to whether the focal species had a territory nearest to the intruder. Note that in tie situations, both species were denoted in the 'No' category. Shaded areas and whiskers indicate 95% confidence intervals

Table 2 The results of the full model (Rank 5 in Table 1) assessing the overall number aggressive responses

Effect	*β*	SD	*z*	*p*
Intercept	4.094	0.4163	9.834	< 0.0001
Black devil	– 0.0140	0.2357	– 0.059	0.95
Moga	0.6633	0.2725	2.434	0.015
Poor man's tropheus	0.4860	0.2469	1.968	0.049
Red breast cichlid	0.4230	0.2405	1.759	0.079
Distance	– 0.0354	0.0049	– 7.191	< 0.0001
Number of territories	– 0.0497	0.1043	– 0.477	0.63

Distance refers to the distance between the intruder dummy and the nearest cichlid territory

of danger', i.e. the probability of being the closest individual to an approaching danger (Hamilton, 1971; McDowall & Lynch, 2019). In this case, nesting close to neighbours is beneficial, but the benefits are not accrued from an increase of defensive aggression with the number of neighbours (which might point to active cooperation), but rather from an increased probability that one of the neighbour territories ends up being the closest one to the approaching intruder, hence carrying the highest risk and burden of defensive aggression. Such behavioural pattern among these fish is further supported by our finding that species-level aggression not only increased by decreasing absolute distance to the intruder but also by the status of being the closest territory defender.

Our results also suggest that the Lake Xiloá species differ in their aggression and, more generally, their role in defining the neighbourhood level of aggression towards the intruder. Here, the intruder appearance may have played a role in the exact pattern of species differences, with previous results suggesting that these cichlids can adjust their aggression to intruder species and appearance (Lehtonen et al., 2015a,b; Sowersby et al., 2018). However, species rankings in absolute levels of aggression (Fig. 1) were not our primary interest, while more general patterns of neighbourhood-wide territorial aggression were not likely to be specific to the intruder dummy we used (black devil). Relative to the other key species, black devil territory holders' role in the overall aggression towards the conspecific dummy was also not particularly large. Aggression by black devil territory holders may have been moderate because of their larger size compared to the other three species that were regularly encountered in this study. In particular, for large species, a lower rate of aggression may already be sufficient for creating a high level of threat that is enough to keep away most intruders (Lehtonen et al., 2011a). Black devils' larger size may also have contributed to how they perceived the intruder: their territorial aggression has previously been shown to positively correlate with the size of the intruder in relation to them (Lehtonen, 2014). Moreover, if black devils are particularly intimidating to their neighbours, or the neighbours perceive them to be that to intruders, their presence might have moderated overall aggression towards the intruder in the neighbourhood. Finally, we cannot exclude the possibility that the presence of an observer might have affected some territory holders more than others.

The differences in neighbours' intruder repellence capacity have potential to affect the local community structure and species co-occurrence (McKaye, 1977a; Lehtonen, 2008, 2019; Santangelo et al., 2024). More generally, different species may generate varying costs and benefits as neighbours, and any biases in their territorial aggression may also affect the difficulty of claiming new territories or later holding them. Once successfully established, neighbours seem to considerably reduce their aggressiveness towards each other (Lehtonen et al., 2010; Lehtonen, 2019), and our hypergeometric tests did not reveal mutual exclusion (or attraction) between any species pairs. Here, future experiments with manipulated exclusions or inclusions would provide more detailed information on consequences of species differences. For instance, even though species co-occurrence patterns in the current study did not deviate from random, whether specific species are overall avoided or preferred as neighbours, relative to their abundance, remains to be experimentally explored. Moreover, in species pairs with a size difference lager than what we observed between the four most common species in the current study (see McKaye, 1977b; Lehtonen, 2008, 2019) co-occurrence patterns might be more biased. At a larger scale, cichlid territories in Lake Xiloá are clustered, which supports the idea of general neighbour benefits (McKaye, 1977a; Semeniuk & Dill, 2006; Quinn & Ueta, 2008; Lehtonen, 2019). The distribution of suitable crevices for hiding eggs and small fry is also likely to contribute to the clustering. Similarly, seasonal variation remains to be assessed. In this respect, at any given time, species may vary in the distribution of the phases of their reproductive cycle. However, given the overall similarity of the breeding seasons of these species, the extensive within species variation in the exact onset date of reproduction, the possibility of more than one brood per season per pair and the commonness of (asynchronously) failed breeding attempts that can be followed by new attempts (McKaye, 1977a; Lehtonen, 2008; Lehtonen et al., 2011a), it is unlikely that seasonal aspects would be a major driver of the observed species differences in aggression.

To conclude, we did not find evidence of cooperation in territorial defence by Lake Xiloá cichlids. Nevertheless, it seems likely that neighbourhoods with tightly packed territories provide some benefits for the residents, with higher overall densities decreasing the investment required per individual, and the neighbour closest to an intruder typically carrying clearly the largest share of defensive aggression, in line with the selfish herd theory. We also found that the array of species forming a neighbourhood matters to the overall rate of aggression towards an intruder, making some species (and potentially phenotypes) presumably better neighbours than others. More generally, such findings suggest that territory defence against intruders can act as a force that shapes the composition of communities. However, the putative role differences between the species were broader than at the level of readily detectable co-occurrence associations between species pairs.

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Data availability Data that support the findings of this study are available as supplementary material (Online Resource 1).

Declarations

Conflict of interest Both authors declare that they have no conflicts of interest.

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