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Societies of the shell-dwelling cichlid *Neolamprologus multifasciatus*

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The cichlid *Neolamprologus multifasciatus* is among the smallest fish in Lake Tanganyika but can dominate areas of the lake floor, living in stable territorial groups with clear memberships that persist for years. This fish is found on 'shell bed' habitats, regions where vast numbers of empty snail shells have accumulated over millennia, preserved by the lake's alkaline waters. Group members take shelter inside the shells that they dig up from the lake floor, aggregating them within their territories with each defending its own shell fiercely, even against much larger rivals, while jointly defending the overall group territory from outsiders. Although miniscule in stature, this fish displays a rich, complex social life in which conflict and cooperation play out against the backdrop of extreme population densities, predation threats, resource defence and ingroup/outgroup interactions. The presence of these fish also imprints itself on the landscape, where their excavation efforts create a cratered, almost lunar landscape on the lake floor, the result of society level territoriality. In the ancient waters of this Lake, these fish are furious with activity, constantly tending to their shelters and engaging in social interactions comparable to the complexity and subtlety of many societies in larger taxa.

The smallest cichlid in Lake Tanganyika, *Neolamprologus multifasciatus*, lives in territorial groups that can carpet the lake floor. Their populations may number in the tens of thousands, and they are found on 'shell beds', regions of the lake floor where millions of empty snail shells of the species *Neothauma tanganyicense* (Viviparidae: Bellamyinae) have accumulated over thousands of years. Groups typically consist of one dominant male living with several adult females and their juveniles, and sometimes along with one or more adult subordinate males as well (Fig. 1a; Bose, Dabernig-Heinz, Koch, Grimm, Sefc, et al., 2022). These small societies live on fixed territories each comprising a cluster of shells that the fish dig up from the sand. While females and smaller males generally stay within distinct and nonoverlapping areas, the dominant male can range throughout the entire area occupied by the group, regularly visiting each shell. Each group member resides within a single 'home shell', where it sleeps, rears young if a female, and shelters from danger (Fig. 1b; Bose et al., 2024). Such groups can consist of up to 22 individuals (Kawanabe, Hori, & Nagoshi, 1997; Bose, Dabernig-Heinz, Koch, Grimm, Lang, et al., 2022; Kohler, 1998) and can be densely packed together, with one study measuring an average of only ~30 cm separating neighbouring territories (Fig. 1c). The distribution of shells on the lake floor dictates where the fish can live and form their group territories, and appears invariant, or at least slow to change, across years. Because shells are often immediately abutting, or only centimetres apart, individuals must find ways to live in close proximity, both within their group territory and in the face of competing nearby groups.

One of several lamprologine species that use empty snail shells in the lake (Lein & Jordan, 2021), the comparatively more complex social life of *N. multifasciatus* is associated with a richer behavioural repertoire, including varied forms of display and de-escalation during contests (Choi & Jordan, 2025). A strict hierarchy defines the members within each territorial group. Dominant males, who can attain a maximum size of 30 mm (Fig. 2), are always the largest fish and dominate smaller society members while being highly aggressive especially towards outsider males as well (Gübel et al., 2021). Coinhabiting females also exhibit a size hierarchy, and larger, more aggressive females are socially dominant over other females. This hierarchy relates to, among other aspects, the quality of shell that each fish resides in as many shells are too fractured to be useful (Bose et al., 2024). The dominant male typically occupies the biggest and most intact shell on the group territory, while other males and females occupy smaller and less

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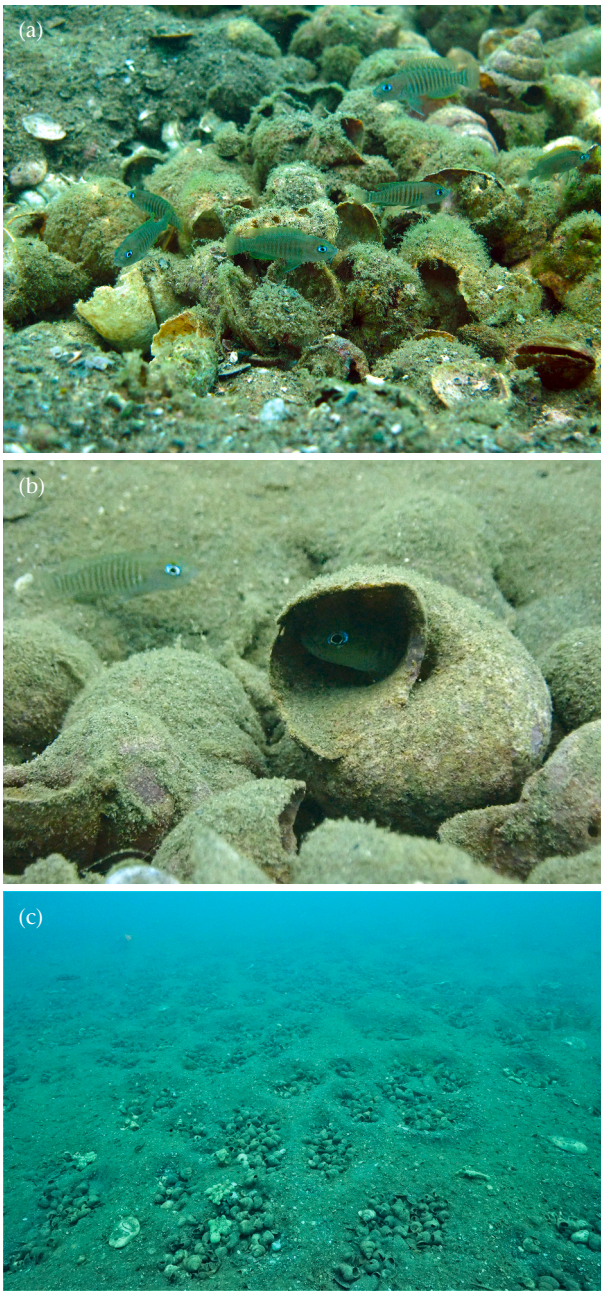

Figure 1. (a) An *N. multifasciatus* group on its territory with dominant female centre, dominant male rear right, and juveniles. (b) A male in his home shell. (c) The cratered landscape of the shell bed showing many group territories.

intact shells, and juveniles inhabit the smallest shells or the crevasses in between them (Bose et al., 2020, 2024). Resource and space limitation is exacerbated by the fact that group territory borders cannot readily be expanded because of the presence of neighbouring groups (a 'saturated habitat'; Jordan et al., 2016).

Shelter limitation in shell bed habitats may seem paradoxical because at first glance shell availability appears nonlimiting, with upwards of 400 shells/m^2 on the shell bed (Soreghan et al., 2024), yet groups in the wild are consistently smaller than those in captive conditions (Jordan et al., 2016). Laboratory experiments have shown clear benefits of owning a larger territory; when additional shells are experimentally added to groups in captivity, the dominant male becomes more attractive to females (Schradin & Lamprecht, 2000, 2002). However, under natural conditions there appear to be two major forces opposing territory expansion. First, increasing shell resources also increases the aggression from neighbouring males, potentially as a form of social policing against exceeding the male's resource-holding potential (Jordan et al., 2016). The second, and likely more profound cost of increasing the number of shells in the territory comes in the form of significantly increased risk of territory loss to larger rivals of the species *Lepidiolamprologus attenuatus*, which likewise occupy shells but apparently cannot uncover and clean those shells themselves, and appear to be attracted to nests that exceed the resource-holding potential of the owner (Jordan et al., 2016). These larger heterospecifics drive out or kill all group members in augmented territories, demonstrating a clear cap on territory size even when resources seem unlimited.

Figure 2. The shell-dwelling cichlid *N. multifasciatus*, also known as 'multis', about 25–30 mm in length in Lake Tanganyika.

Territory and border conflicts are front and centre in the social lives of these fish. Dominant males traverse and defend the entire territorial space of the group, which typically spans up to ~200 cm^2, while other group members remain largely confined to their individual territories; those held by females are nonoverlapping and form distinct sectors within the overall group territory (Bose et al., 2021). Nevertheless, multiple members may join in defence against group territory intruders, and must do so within seconds to ensure group safety, in a response often orchestrated by the dominant male and whichever individual's territory is closest to the approaching intruder (Gübel et al., 2021). Within the group territory, female–female conflicts break out commonly when one female enters the space of another, especially when there are also young offspring present, and when this happens the dominant male often intervenes by aggressing against one of the females or positioning himself in between them, apparently to de-escalate the conflict (consistent with 'peacekeeping behaviour'; Bose et al., 2021; Schradin & Lamprecht, 2000). Within-group aggressive contests are more likely to occur between fish whose home shells are situated closest to one another, especially among unrelated females (Bose et al., 2023), and are most commonly expressed as ritualized displays rather than overt aggression, although these can escalate to biting that leads to torn fins and open wounds. Nevertheless, *N. multifasciatus* can also resolve conflicts, either directly or via peace keeping from other group members, and thus cohabit in small spaces. However, disruption to the typical societies can alter these patterns; laboratory studies have shown that if a dominant male dies and is not immediately replaced by a new one, infighting among females over shells and individual territory space will result

in some females evicting others from the group (Schradin & Lamprecht, 2000). In the wild, however, it is likely that a subordinate male from the same group territory, or moving in from a neighbouring one, will ascend to dominance; or alternatively that females will become incorporated into a neighbouring group (Bose, Dabernig-Heinz, Koch, Grimm, Lang, et al., 2022).

Most territorial groups are stable and persist in the same location over months, but likely also across years, and perhaps even greater than the life spans of the fish (ageing of sagittal otoliths has estimated that some males in the wild live to at least 10 years old; Bose et al., 2025). While the membership may change due to predation or internal turnover of dominance, the location and paternal lineage of a group remains intact due to within-group ascension of subordinate males. This stability is likely supported by ecologically constrained dispersal and territorial inheritance. On average, males are more closely related within their groups (average relatedness of 0.23 ± 0.27) than females are to one another (average relatedness of 0.045 ± 0.15; Bose, Koch, et al., 2022). Males also show elevated relatedness to other males in nearby groups, but only up to ~2 m away. Together, this suggests that males are highly philopatric, potentially inheriting their natal group territory, such that group territories may persist through generations as a form of ecological inheritance. Females more readily emigrate to new groups, but even they can struggle to disperse farther than the neighbouring territories (i.e. more than 2 m away; Bose, Koch, et al., 2022). Given the vulnerability of these small fish to predation when venturing away from their shells, long-distance dispersal is likely exceptionally rare (the farthest distance measured to date between a young fish and their parent in the wild has been ~4.5 m; Bose, Dabernig-Heinz, Koch, Grimm, Lang, et al., 2022). Resource availability appears to be a motivator behind female-biased dispersal as females are more likely to emigrate when a group controls only a few shells (Schradin & Lamprecht, 2000). Females also face less resistance than males when immigrating; although resident females try to aggressively resist the entry of newcomer females, their dominant male often intervenes to suppress this defence (Gübel et al., 2021). It is currently unknown just how many juvenile individuals ultimately attempt dispersal, the likelihood of their acceptance by a new group, or whether individuals disperse more than once per lifetime.

A consequence of living under intense ecological constraints is that group members have very limited opportunities for reproduction outside of their group, and nearly all offspring are sired by the dominant male (Bose, Dabernig-Heinz, Koch, Grimm, Lang, et al., 2022), leaving subordinate males to queue for available higher hierarchy positions in their group. However, the genetic structure of populations tells us that males do at least occasionally emigrate, with Jordan et al. (2016) observing individual males attempting to establish their own territories or to move into neighbouring groups, They start by swimming a short distance outside their territory, and slowly excavating a nearby shell , although initially they retreat back to their natal territory whenever danger approaches (Jordan et al., 2016). Once they have emptied a shell, they begin to excavate additional shells, presumably to increase territory quality and attract females, who may then themselves being to excavate additional shells. However, this process seems to carry great risks, and these nascent groups often disappear within weeks, presumably falling victim to predation or aggression from surrounding territorial groups. Subordinate males therefore seem constrained by dispersal opportunity or predation risk to live with a dominant male and occupy valuable space on his territory; future research is needed to understand why dominant males tolerate this. While it does not appear that subordinate males provide any direct alloparental care, their presence in a group may be tolerated due to kin selection (when they are related to the dominant male) or other group level processes such as increased defensive capacity against unrelated conspecifics, egg predators or territorial heterospecifics, as well as potential benefits of predation dilution or increased vigilance, which may counteract any costs to their presence.

Neolamprologus multifasciatus also cooperate, although in most cases these behaviours are more easily classified as 'mutually beneficial' than 'altruistic'. Previous literature has referred to *N. multifasciatus* as a cooperative breeder, but concerted observations over the past decade have yielded no evidence that any individual other than the mother cares for her offspring, which stay in her shell until they are old enough to find a shell of their own. In addition to jointly defending against intruders, all group members also engage in maintenance of their space by removing sand that accumulates over time, although each fish concentrates on clearing the area around its own home shell. Sand is scooped up in the mouth and then spat out along the borders of the group territory to create sand ridges or buffer zones between themselves and neighbouring social groups (although sometimes group members also spit sand at each other, a potentially competitive behaviour that warrants future attention). While research is still ongoing, our current assessment is that these fish also benefit from the 'many-eyes effect', using social cues to detect threats from larger predators that pass over territories in search of juvenile fish as prey, and perhaps situating their group members in arrangements that maximize visual fields.

It is clear from experiments exploring the 'Dear Enemy' effect that territorial aggression is influenced by familiarity at the boundaries of the group territory: known neighbours are tolerated by both sexes with minimal aggression, but unfamiliar neighbours are physically attacked (Lein et al., 2025). However, even familiar neighbours will be met with intense aggression when they violate territorial boundaries. It is therefore clear that *N. multifasciatus* recognize individuals and have specific rules of tolerating known and unknown individuals belonging to other territorial groups, suggesting developed sociocognitive skills. The mechanisms by which individuals distinguish one another are not well known, but evidence from related species suggests visual markings on the body or face are used (Kohda et al., 2015). Indeed, the individual barring pattern that gives the species their name (multifasciatus means 'many striped') may be a useful cue in recognizing members of each society. Future work exploring the sensory modalities used in categorizing others and social communication in this species should reveal much about the mechanism underlying the maintenance of their societies.

Empirical data on the complex and varied social lives of Lake Tanganyika cichlids is accumulating rapidly, and these species have already been put forward as an excellent model for studying societal evolution (Lein & Jordan, 2021). Among the shell-dwelling lamprologines, *N. multifasciatus* stands out as a prime candidate in studying social and behavioural evolution. Within a population, there can be large variation in group structure, from single males attempting to begin new territories, to pair-bonded breeders defending a handful of shells, all the way up to large groups with overlapping generations. Future work can leverage this variation to explore many facets of societies and social living, from the differences in behavioural repertoire among individuals living under different levels of social complexity to changes in neuroanatomy associated with differences in social experience (e.g. Ma et al., 2025) by looking within a single continuous population. Because this species can also be readily kept in the laboratory, experiments can also manipulate social structural and ecological factors that are known to vary in the wild, elucidating the costs and benefits of behavioural variations in a controlled manner. This species has extreme site fidelity, and so modern approaches to animal pose and movement tracking can be applied in field settings (Bose et al., 2021; Francisco et al., 2020), linking situated

analysis of ecological and evolutionary processes with modern quantitative techniques, and can be performed over months and even years due to the long-term stability of social units. Because every individual carries a specific barring pattern, automated identification is also achievable (given sufficient video resolution) without the need to catch or otherwise manipulate individuals, providing a near-perfect system in which to gather data on natural social interactions over extended periods.

Overall, the current knowledge on 'multis' (i.e. *N. multifasciatus*) reveals this species to be a highly combative, societal fish, living in a landscape constrained by resource availability and predation risk. This small species can make large changes to its habitat by modifying the landscape through shell excavation and pass long-lasting territories on to subsequent generations. Although a humble fish living in a remote lake, *N. multifasciatus* provides us with a vibrant and tractable system to study and compare with other species across the animal kingdom and continues to generate novel insight into the evolution and ecology of animal societies.

Author Contributions

Alex Jordan: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Etienne Lein:** Writing – review & editing. **Bin Ma:** Writing – review & editing, Investigation. **Aneesh P.H. Bose:** Writing – review & editing, Writing – original draft, Visualization.

Data Availability

No data were used for the research described in the article.

Declaration of Interest

None.

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