Cichlids as a Model System for Studying Social Behaviour and Evolution

Alex Jordan, Barbara Taborsky, and Michael Taborsky

Abstract The complex social behaviour of cichlids has fascinated scientists and hobbyists alike for almost 100 years. In this chapter, we review the breadth and complexity of cichlid behaviour, particularly with respect to social interactions. We present the case that cichlids are one of the best model systems for understanding both the mechanisms and evolution of behaviour. This is due to the fact that cichlids can be observed without being greatly disturbed, both in the aquarium and field and because of the unique opportunity to experimentally manipulate their environment and behaviour. We first give a brief account of the diversity of social systems in the cichlids and the diverse research in this area, from the very early work of authors like Curtis, Noble, and Baerends, to modern studies into the dynamics and structure of social behaviour in these fish. In Sect. 2, we explore the causal factors leading to the evolution of social complexity, discussing the occurrence and evolution of different social systems across ecological and life-history contexts. We investigate the behavioural complexity displayed by cichlids in Sect. 3, including a brief treatment of the different modalities of behavioural interactions. In Sect. 4, we discuss the immense potential for using cichlids as model species in studying social and behavioural evolution, before ending in Sect. 5 with exciting future directions for research employing the latest technical advances in both the laboratory and field.

Keywords Social organisation · Behavioural diversity · Mating · Communication · Plasticity

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1 The Beautiful Complexity of Cichlids

For the unacquainted, fish may be considered to be simple, anonymous, vacant, or unthinking entities; the apocryphal tale of the goldfish and its three-second memory is testament to this common perception. When we consider vast schools of sardines moving through the water, following relatively simple interaction rules, and moving as a cohesive unit, it is not hard to see how the idea of simplistic fish behaviour has emerged, especially when compared to the subtle and varied behaviour of primates and other mammals. In fact, pelagic species that live in open water may often have low-complexity behavioural repertoires, as they exist in fission-fusion groups in which the primary ecological pressures—feeding and avoiding predation—require highly conserved and stereotypical behavioural patterns that promote aggregation. These pressures may lead to a specialised form of social interaction, that of collective behaviour, in which synchrony and conformity are prioritised as strategies to avoid predation, hunt, or share information (Gordon 2014). In many of these species, even mating is typified by relatively anonymous synchronised release of gametes into the water column (Takemura et al. 2010). While large groups of almost identical animals moving and behaving in synchronisation are certainly capable of producing complex emergent behavioural patterns, at the level of the individual agents—be they mammals, birds, or in our case fish—there is a relatively small behavioural rule set by which they act (King et al. 2018).

But then consider the cichlids. These fish commonly live in stable social groups with repeated interactions and show highly developed behavioural responses to encounters with mates, social partners, rivals, and competitors, including heterospecifics (Taborsky 1984; Martin and Taborsky 1997; Balshine-Earn et al. 1998). In addition, the cichlids also have highly developed socio-cognitive abilities, including memory of past social interactions, facial and kin recognition, and commodity trading (see Félix and Oliveira 2021). Almost every aspect of the interaction between cichlid fishes consists of a wonderful array of postures, colour changes, fin movements, and reciprocal behaviours. Ethograms for cichlids range from 20 to 50 discrete behaviours, spanning aggression, courtship, social affiliation, and punishment. The 'language' of cichlid behaviour has fascinated both naturalists and ethologists for almost 100 years, with early researchers like Breder (1934), Noble and Curtis (1939), Baerends and Baerends-van Roon (1950), and El-Zarka (1956) publishing some of the first studies on the amazing diversity and complexity of cichlid behaviour. More recent syntheses have further cemented the evidence for cichlids as some of the most fascinating and complex animals on the planet (Keenleyside 1991; Barlow 2000).

The social systems of cichlids also include a vast range of levels of social organisation. The so-called 'sardine cichlids' of the genus *Cyprichromis*, for instance, live in vast pelagic fission-fusion shoals and resemble the ecology, behaviour, and social systems of pelagic marine species (Ochi 1996). Nevertheless, even these Cyprichromine species show more social structure than basic fission-fusion, at least during mating and lekking, during which males may defend open-water

3-dimensional 'territories' and be spatially isolated from shoaling females and non-breeding males (Konings 2015). The 'mbuna' (algae scrapers) of Lake Malawi, as well as some Lake Victorian haplochromines, Lake Tanganyikan *Tropheini*, and the *Geophaginae* in the Americas have itinerant feeding behaviour and often forage in large groups, but may also have temporary territories during breeding periods or defend semi-permanent feeding territories (Kohda 1991; Yanagisawa and Nishida 1991; Genner and Turner 2005). These territories are commonly held by males, who may court passing females from a flat rock or an area cleared of debris. Males are highly territorial during these periods and may form dear-enemy relationships with neighbouring males. After breeding, the mouthbrooding females re-join itinerant fission-fusion shoals. Finally, there are a great many substrate spawning cichlids, best represented in the tribe Tanganyikan Lamprologines and West African and South American riverine species that live in long-term social units. The Lamprologines, in particular, show the greatest variety of social systems known in any group of fish (Kuwamura 1986). These cichlids may live in pairs, harems, or even social groups numbering up to 50 individuals, and they display many of the social attributes once held to be the realm of mammalian societies, especially primates (Heg and Bachar 2006). This includes, for instance, reciprocal trading of different commodities among group members, such as access to defended resources against help in brood care and territory maintenance (Taborsky 1985; Heg and Taborsky 2010; Zoettl et al. 2013b; Naef and Taborsky 2020).

The value of studying cichlids in the context of evolutionary biology has long been recognised (Kornfield and Smith 2000) and progress in understanding the morphological, genomic, and ecological processes involved in speciation continues apace (e.g. see Wagner 2021 and other chapters in this volume). Yet our understanding of how behaviour evolves is still relatively poor, not only in cichlids, but across taxa and disciplines. Cichlids represent an incredibly powerful system in which to interrogate and explore behavioural evolution (Rossiter 1995). In this chapter we will demonstrate the value of cichlids as models for understanding the evolution of social behaviour, highlighting the progress in this area and outlining future avenues for further work.

2 Cichlid Social Groups

In this section we summarise the major forms of social organisation in cichlids, presenting evidence for the potential causative factors leading to different social structures. We go on to explain in detail the life-history consequences of different social arrangements across cichlids, with a particular focus on the Lamprologine cichlids of Lake Tanganyika.

2.1   Ecology: Defendable, Stable Resources

When considering the evolution of social behaviour, it is helpful to consider how the physical structures that individuals live in and around, and the resources they use, can affect the frequency and nature of interactions among group members. The link between the behaviour—especially social behaviour—and physical structures is perhaps best exemplified by the nests of social insects, where the structure is both a cause and consequence of social behaviour. Yet this link is true for many other relationships between space, structure, and behaviour. In cichlid species that utilise ephemeral and mobile food resources, such as plankton blooms, or those that live in streams or rivers where food is brought in by currents, there is no single area in which individuals will permanently gather to access food. As such, fish species that utilise transient, ubiquitous, or unpredictable food resources may be less likely to develop complex social behaviours, as scramble competition may be the best response to such environments. There is also little benefit in the defence of ephemeral food patches. The primary benefit of living in groups when food is transient more likely comes through processes such as predation dilution and increased vigilance. In such cases, groups, when they do form, are more likely to exist as fission-fusion shoals without stable membership or group sizes, and are likely to be itinerant in their search for food resources. In cichlids, the vast majority of Haplochromines do not have stable feeding territories and these and many other cichlids instead form large shoals of females and non-breeding males that continually move within a larger general feeding area. An exception to this itinerant lifestyle is resident groups of juveniles, young-of-year, or conglomerates of similar size heterospecifics, typically numbering between about 50 and a few hundred individuals (*Perissodus microlepis, Neolamprologus caudopunctatus, Lepidilolamprologus attenuatus*), which form apparently locally stable groups for unknown lengths of time (Jordan and M. Taborsky pers. obs.). These groups may arise from a single brood that has moved from the parental breeding territory (or may stay within or above it), but can also form as apparently ad-hoc groups of different species brought together through a common resource (e.g. a semi-stable current-carrying plankton plumes). Similarly, the Lake Tanganyikan genus *Cyprichromis* forms massive pelagic groups numbering in the thousands, which aggregate around structures such as vertical rock walls. Similarly, large heterospecific groups of *Simochoromis* and *Tropheus* aggregate on algae-covered stone outcrops in shallow water, although the degree of site attachment in these and other fission-fusion shoaling species is difficult to judge.

In contrast, when resources are static and defendable, permanent, stable home ranges occupied by small groups, pairs, or single individuals are more common. One form of site attachment comes in the form of defended feeding territories. For example, some species that feed on Aufwuchs ('turf' or algae-covered stones), which they defend as feeding territories either permanently or during mating and breeding. In Lake Malawi, *Pseudotropheus elongatus* adult males, females, and large juveniles defend a feeding territory (Ribbink et al. 1983), while in the

Tanganyikan *Tropheini*, single individuals defend 'algae gardens' either for feeding themselves or additionally to attract mating partners (Kotrschal and Taborsky 2010). Some *Eretmodini* form lifelong, stable pairs that jointly defend an algae patch as an all-purpose territory (Taborsky et al. 2014) while in *Neolamprologus obscurus*, the territory serves as both a breeding resource and a food catchment area (Tanaka et al. 2016). These territories may be permanently defended, or defence may be temporary, as in the case of *Gnathochromis pfefferi*, which defends a breeding territory during the morning and a separate feeding territory during the afternoon (Barlow 2000). Despite these examples, defence of a permanent feeding territory is relatively rare, perhaps due in part to the intractability of defending the ephemeral food resources used by many cichlids.

More common are territories based around shelters and breeding sites, which are more temporally and structurally stable resources (e.g. Brown 1964), especially in substrate brooding cichlids. In New World and riverine cichlids this may take the form of a submerged log or rock, while in Old World and lake cichlids it may be a crevice among the rocky shore, empty snail shells, or a chamber dug out from under stones and boulders. Among social groups, competition for these shelter sites can be intense, and inter-group rivalry can create physical borders between group territories. For example in the shell-dwelling *N. multifasciatus*, neighbouring groups continually dig out sand from within their own territories and deposit it on or over the edge of their borders (Sato and Gashagaza 1997; Jordan et al. 2016). This is often directly deposited into the territory of another group, in which the behaviour is perpetuated, leading to the development of sand drifts along the territory boundaries. These boundaries create clear physical partitions among social units of this species, which are reflected in the social structure (Fig. 1). A paucity of suitable shelter sites may also lead to increased sociality by delaying dispersal decisions. For example in *N. pulcher*, dispersal of juvenile helpers is limited by predation risk (Taborsky and Limberger 1981; Taborsky 1984; Heg et al. 2004a). Experimental provisioning of potential territories to wild communities does not cause subordinate group members to leave their group and establish their own territories when these territories were placed at the edge of a colony, but territories placed within the colony were readily claimed and inhabited by both *N. pulcher* and the syntopic *N. savoryi* (Heg et al. 2008). Moreover, when attractive positions were experimentally created within neighbouring territories, some individuals chose to switch groups after intensifying exploration of such groups (Jungwirth et al. 2015). Laboratory experiments revealed that dispersal decisions are influenced by both availability of alternative breeding sites and the quality of the home territory (Bergmüller et al. 2005). Nevertheless, habitat saturation is not essential to delay dispersal; when alterative dispersal options are experimentally presented, even unrelated subordinates may prefer to stay with dominants (Taborsky 1985; Heg 2010). This may be related to the tendency for helpers to join large groups and groups containing more dominant individuals, even though joiners incur greater aggression and reduced chances of inheriting the territory in these groups (Jordan et al. 2010a; Reddon et al. 2011a), suggesting a primary function of group membership is protection against predation (Taborsky 1984).
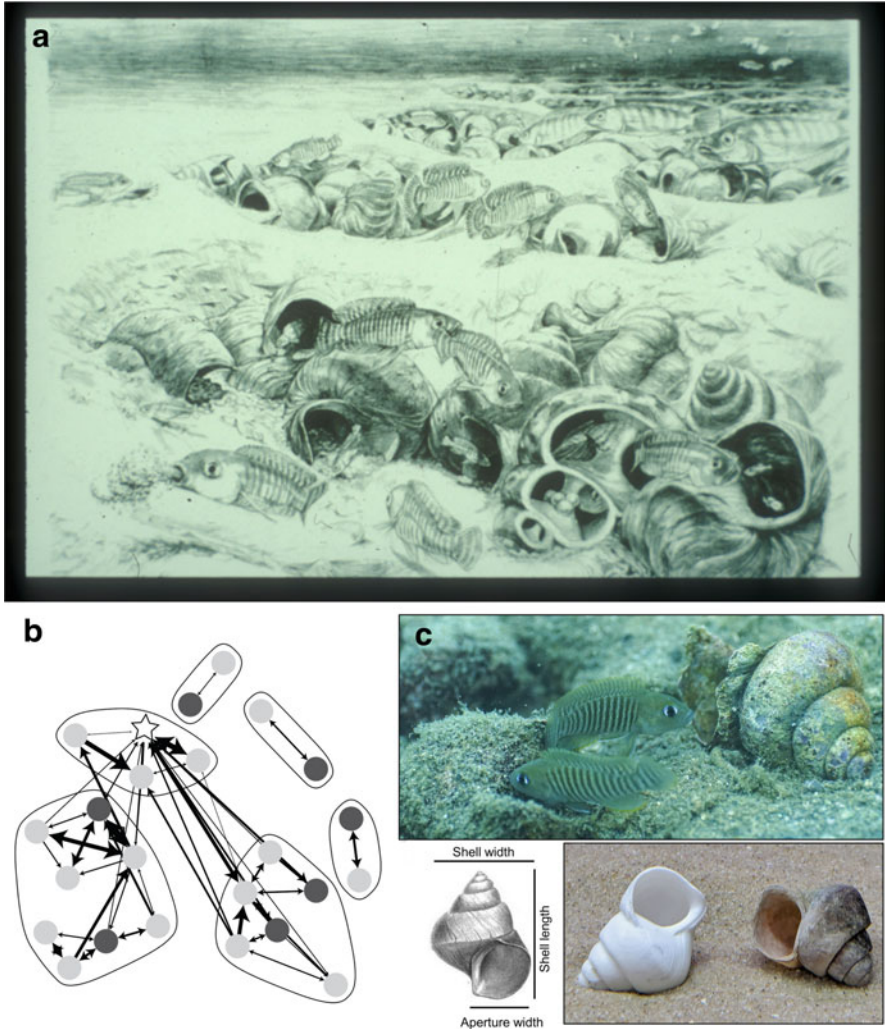
Fig. 1 The shell-dwelling Tanganyikan cichlid *Neolamprologus multifasciatus* lives in large communities composed of hundreds of social groups, typically containing between 2 and 10 members, but in some cases up to fifty individuals. (**a**) in these communities, groups rear young within shells, defend against predators, perform courtship and aggressive displays, and forage for food (illustration by Uwe Kohler), (**b**) these groups are composed of individuals that perform repeated social interactions, and are highly amenable to social network analyses like those performed in Jordan et al. (2016), (**c**) within these groups, individuals compete over resources, including empty *Neothauma* snail shells, the structure of which mediates preferences, as revealed using scanning and 3D printing of shells in Bose et al. (2020)

2.2 From Fission-Fusion to Long-Term 'Closed' Groups

The temporal social dynamics of animal groups can have far-reaching consequences for the behaviour of individuals within them. One of the major differences among animal groups is the degree to which individuals can move among groups and the residence times within each group (Jordan et al. 2010a). On the one extreme are fission-fusion systems, in which groups may form and dissolve in a matter of seconds. A classic example is that of guppy shoals in Trinidad, which may be composed of a hundred or so individuals, but in which each individual may only remain for a brief time before joining another shoal (Croft et al. 2006). The social environment in which an individual exists is therefore highly transient, and the likelihood that two individuals will have repeated interactions is reduced. This can also be true for very large schools; marine species such as sardines can number in the thousands, effectively eliminating the possibility for repeated social interactions among the same social partners. In these large schools, the role of the individual is relatively diminished, and all individuals are likely to react and behave in a collective manner (Parr 1927).

In cichlids, this type of fission-fusion social system is found among many pelagic species that have itinerant feeding territories based on local plankton (e.g. *Cyprichromis*), or which travel over rocky substrates grazing on algae (Malawian mbuna, *Petrochromis spp., Geophagus spp.*). Moreover, many species transition between group states, forming fission-fusion shoals either at specific life stages (e.g. non-reproductive *Lamprologus callipterus* and *Boulengerochromis microlepis*), or depending on their reproductive state (e.g. non-reproductive 'subordinate' males joining shoals of females in *Astatotilapia*). This form of social arrangement is best represented in the pelagic and above-littoral zones, where no natural cover exists and shoaling is an effective behavioural strategy to reduce predation risk. In Lake Tanganyika there are relatively few cichlids in the pelagic zone (e.g. the largest of all cichlids, *B. microlepis*, and members of the genera *Hemibates* and *Bathybates*), but this niche is mostly populated by two non-cichlid species, the endemic clupeids, *Limnothrissa miodon* and *Stolothrissa tanganicae*, known locally as 'kapenta', as well as their primary predators, the Nile perch species *Lates angustifrons*, *L. mariae, L. microlepis* and *L. stappersi*. In the open-water areas above rock and sand in Lake Tanganyika, shoaling and schooling cichlids in fission-fusion schools are common, and best represented by solitary or small groups of *Cunningtonia, Opthalmotilapia, Cyathopharynx, Cyphotilapia*, or very large schools of *Cyprichrominii* (Rossiter 1995).

At the other end of the social spectrum are groups in which membership is stable over long periods, where individuals form pairs, harems, or larger social groups (Fig. 2). These social structures are most commonly associated with rocky and intermediate rock/sand habitats including crevices, exposed rocky surfaces, sand patches interspersed with rock, as well as vast beds of fossilised *Neothauma, Paramelania,* and *Lavigeria* snail shells. The physical structures in these habitats are used as spawning and shelter sites by many Lamprologine species (Gashagaza
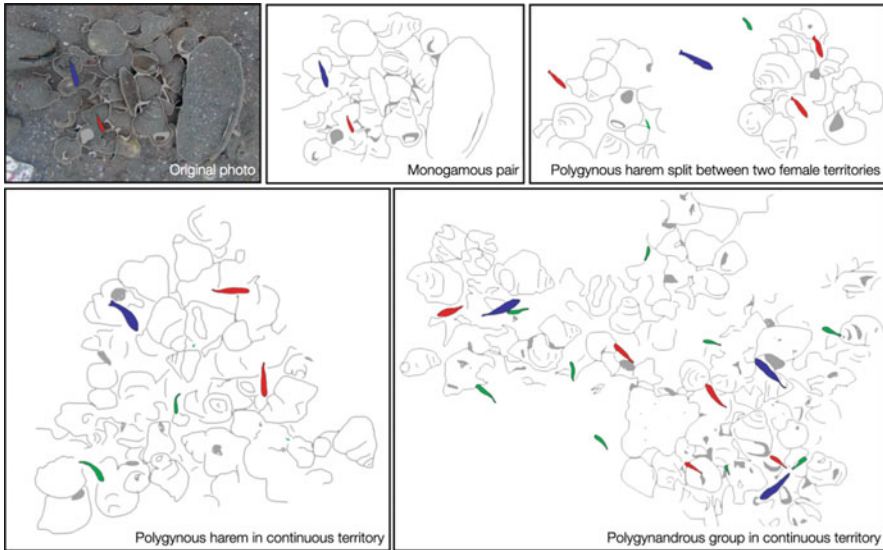
Fig. 2 Social organisation can vary greatly within and among species depending on factors like resource availability and predation risk. At Chikonde Bay, Zambia, *N. multifasciatus* lives in social groups ranging from pairs up to polygyndrous groups. Outlines of shell territories in grey, males in blue, females in red, and juveniles in green (Figure by Alex Jordan)

et al. 1995), and also serve as feeding sites (Hori 1983; Kuwamura 1992; Kohda and Yanagisawa 1992; Tanaka et al. 2018b). In Lake Tanganyika, almost 65% of cichlid species are associated with these rocky habitats (Rossiter 1995), and it is the species in these regions that have received the most attention by behavioural researchers. Work on the species *Neolamprologus pulcher* has shown that aggression prevents free movement of individuals among groups, as individuals attempting to join groups may be repelled by resident members if their help is not needed (Zoettl et al. 2013b). When movement among groups does occur, it is preceded by an extended period of prospecting behaviour, in which an individual will frequently visit a group over a period of weeks or months before finally being accepted (Bergmüller et al. 2005; Zoettl et al. 2013a; Jungwirth et al. 2015). Much like many mammalian social systems, these 'closed' groups are characterised by iterated social interactions, well-established social dominance hierarchies, and varying degrees of intra-group relatedness (Taborsky 2016b).

The distinction within cichlids of these two generalised life-history strategies was long ago described as the 'school' and the 'territorial society' social states and were considered to be labile as a function of development or breeding status (Baerends and Baerends-van Roon 1950). *Lamprologus callipterus* represents a particularly striking example of this lability, with packs of non-breeding individuals forming large schools of itinerant collective hunters, some of which then ontogenetically shift to become territorial as breeders occupying shell beds (Sato 1994; Schuetz et al. 2010). Within the Great Rift Lakes, predation risk can be a major determinant of

social structure in both fission-fusion and more stable groups. In Lake Tanganyika, the historical presence of large piscivorous species has promoted collective anti-predator behaviour in many pelagic species. However, fission-fusion groups are less well-represented in Malawi and Victoria, which have until recently lacked such large predators (Coulter et al. 1991; Rossiter 1995). In stable group-forming species, predation pressure can also lead to changes in group structure (Groenewoud et al. 2016). At a more general level, the debate about the role of predators inhibiting or promoting speciation is long-standing (Worthington 1937, 1940; Fryer 1959, 1965; Jackson 1961).

While many social groups form to decrease the risk of predation or increase the likelihood of successful resource defence, groups may also form to overwhelm the defence of territory holders. In species such as *Petrochromis spp., Simochromis spp.*, and *L. callipterus*, foraging groups may be able to overwhelm the territorial defence of other species (Kohda and Takemon 1996). In these species, groups move into a territory to feed on algae cover or benthic invertebrates, and while they are attacked by residents, their numbers are too great for the group to be repelled and the per capita risk of attack is greatly reduced, so that individuals within these groups can successfully exploit the feeding territories of other species. This strategy has been called the 'Saint Ignatius strategy' due to the increased likelihood that an aggressive act from a territory owner will befall a social partner or 'friend' (Paradis and Williams 2014), constituting a form of risk dilution accrued to individuals in groups or aggregates. As pointed out by Barlow (1974a, b, 2000), these groups are functionally similar to groups of coral reef herbivores, such as the T-shirt surgeon fish (*Acanthurus triostegus*), which move through feeding territories of other fish in large roving bands.

An extended form of sociality occurs when stable arrangements of heterospecifics form around defended resources, as observed for instance in herbivorous (algae-feeding) cichlids in Lake Tanganyika (Kohda 1991). In these cases, it has been argued that hierarchy and social relationships may form between members of different species in much the same way as for conspecifics, i.e. through repeated interactions based on site attachment and resource defence. Indeed, size-dependent heterospecific hierarchies were observed between two *Tropheus* species, as well as up to five species of *Petrochromis*. Alternatively, these heterospecific interactions may take on a different valence and become cooperative, as in algae grazing *Petrochromis polyodon* and *Tropheus moori*. While these species have overlapping territories containing algae mats, they are rarely aggressive towards one another, potentially because *P. polyodon* feeds primarily on unicellular algae while T. moori feeds on filamentous algae, and so competition is reduced. Cooperation occurs as mutual defence of the territory, and benefits may arise to *T. moori* also from feeding being facilitated by the scraping action of *P. polyodon* (Kohda 1995). Although we are not aware of scientific documentation of this phenomenon, a form of cooperative hunting is also observed between *Lepidiolamprologus elongatus* and some species of Mastacembalid eel in Lake Tanganyika, in which heterospecific pairs form and hunt through rocks and shell beds (A Jordan and M Taborsky pers. obs.)

2.3 Reproduction

There are two main modes of reproduction in cichlids that have a great influence on the likelihood of social systems and behaviours developing. Substrate brooding, in which eggs are laid on an external surface and guarded where they are laid in situ, and mouthbrooding, where eggs and fry are taken into the buccal cavity and reared therein for a period up to a few weeks. Tanganyika is unique among the African Great Lakes in possessing indigenous representatives of both groups; the endemic cichlids of Lakes Malawi and Victoria are all maternal mouthbrooders (Fryer and Iles 1972; Greenwood 1974; Ribbink et al. 1983). These two groups show fundamental differences in their breeding mode and ecology. Substrate spawning usually involves strong territoriality, a firm pair-bonding, and guarding of eggs and young (Kuwamura 1986; Nagoshi and Gashagaza 1988). In contrast, mouthbrooding is most commonly performed by only one sex, typically the female, and does not involve strong territoriality (Yanagisawa and Nishida 1991).

Mouthbrooding is common (Fig. 3) and widespread in the Cichlidae in both Old and New World species, and while it is most commonly performed by females, it may be performed by either sex (Kuwamura 1986), or even by both as in *Microdontochromis rotundiventralis* (Yanagisawa et al. 1996) and *Eretmodus cyanostictus* (Grüter and Taborsky 2005; Steinegger and Taborsky 2007; Taborsky et al. 2009). The existence of the pharyngeal jaws has relaxed selection on the mouth as a food processing unit in the cichlids, facilitating the development of a buccal cavity in which fry can be reared. This mode of parental care means that outside the actual event of fertilisation, cichlid parents do not need a substrate in which to defend eggs or need to provide shelter to young. The mouth provides all the protection the young need, even supplying a mobile shelter into which fry can retreat at a moment's notice of danger from the parent. Because of this, once they have mated, individuals that are carrying eggs or fry can immediately re-join fission-fusion shoals and do not need a substrate in which to protect and shelter the brood. The evolution of mouthbrooding can thus be considered a pre-adaptation for lacustrine living because it immediately releases care-giving species from an obligate association with the benthos. Mouthbrooding is considered a causative factor in the success of cichlids in the vast African Rift Lakes, where hundreds of species have radiated from a small number of founding species. Because there is no need for long-term territories in mouthbrooding species, it is frequently only the male that defends a bower or breeding site at which courtship and mating occur. These are transient territories, typically assembled in leks, that last only as long as the male owners are in breeding condition, during which time they may sire broods with numerous females before returning to a transient feeding life stage. This type of breeding system occurs, for example in the Lake Tanganyika cichlids *Cyatopharynx furcifer* (Schaedelin and Taborsky 2006, 2010), *Ophthalmotilapia ventralis* (Immler and Taborsky 2009) and *Simochromis pleurospilus* (Kotrschal and Taborsky 2010).

Not all mouthbrooding species are lek-breeding and promiscuous, however. There are species that form permanent or semi-permanent social bonds
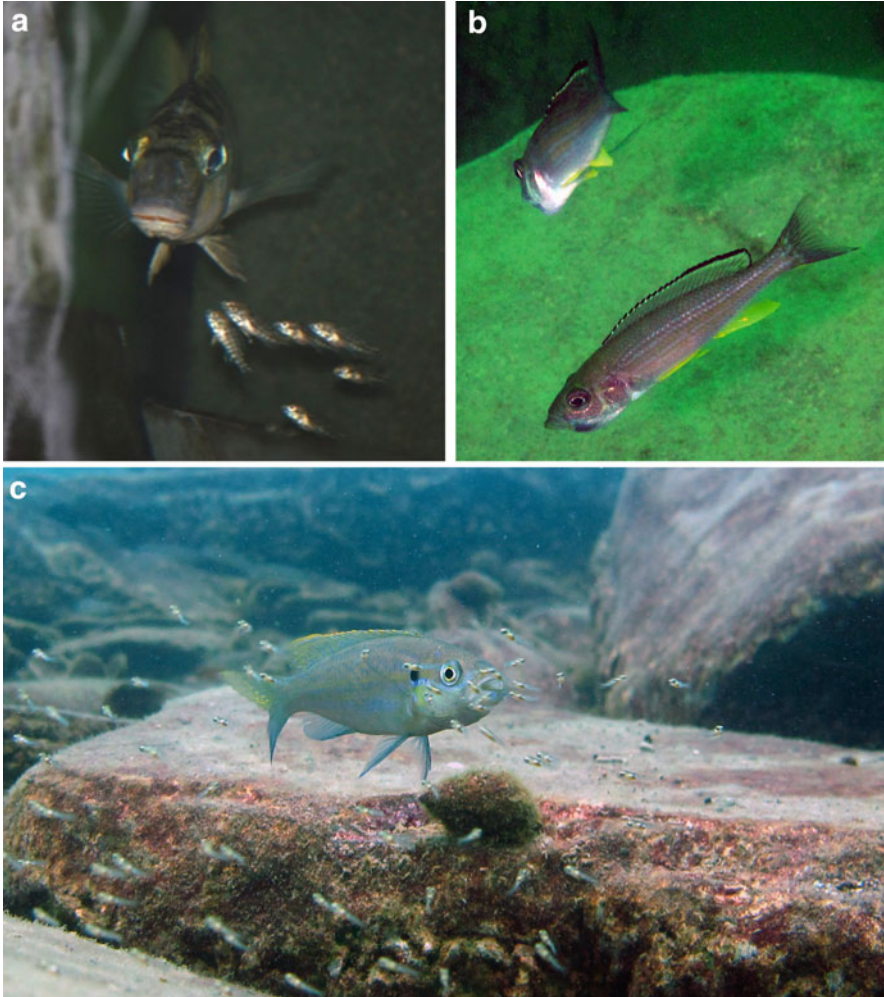
Fig. 3 Mouthbrooding in cichlids. (**a**) a female *C. pleurospilus* recalling her young into the buccal cavity due to perceived threat (photo F.H.I.D. Segers), (**b**) female *Cyprichromis coloratus* form large shoals while mouthbrooding eggs and young (photo Alex Jordan), (**c**) both male and female *Perissodus microlepis* provide care of young, here young retreat from the substrate into the mouth of the guarding parent (photo Alex Jordan)

co-occurring with more complex mouthbrooding behaviour such as biparental mouthbrooding. A female-to-male shift of young is known in several monogamous mouthbrooding cichlids of Lake Tanganyika; e.g. *Eretmodus cyanostictus, Tanganicodus irsacae, Asprotilapia leptura, Xenotilapia flavipinnis, X. boulengeri, X. longispinis, X. spilopterus* (Kuwamura 1986; Yanagisawa 1986; Grüter and Taborsky 2005; Steinegger and Taborsky 2007; Sefc 2011). The transfer of young may be a mechanism to reduce the period of time that females spend

without feeding, potentially allowing them to return to breeding condition more quickly. This explanation would only be evolutionarily stable if the pair-bond remained stable over an extended period, during which the male's fitness was defined by his association with the female and he was certain of paternity. A lack of pair fidelity (arguably true for *E. cyanostictus* in which pairs are stable for circa 1.5 breeding cycles; Taborsky et al. 2009) would reduce the male's payoffs from parental investment and leave biparental mouthbrooding at risk of being lost in evolutionary time. Accordingly, in *E. cyanostictus*, there is intensive sexual conflict over the burden of parental care around the time when the females signal the male that she is ready to transfer the young (Steinegger and Taborsky 2007). Another Tanganyikan species, *M. rotundiventralis* also displays biparental mouthbrooding, although parents only swap a portion of the brood, apparently to aid in intrabuccal feeding of the young rather than reduce the care period (Yanagisawa et al. 1996). Maternal mouthbrooders employ either a semalcavous or iterocavous strategy— either releasing fry permanently after a fixed period of mouthbrooding, such as *Stomatepia pindu*, a West African Crater Lake cichlid or allowing fry to re-enter the buccal cavity when danger appears, as in many Rift Lake species including *Haplotaxodon microlepis* and species of the subfamily of *Tropheini* and the genus *Xenotilapia* (Kuwamura 1986).

The alternative parental care system, substrate or crevice brooding (Fig. 4) is the ancestral state and requires a territory in which to spawn and protect eggs and fry (Kuwamura 1986). As outlined earlier, these territories often constitute a stable defendable resource from which repeated social interactions can arise, either with stable neighbours in a permanent breeding territory or shorter-term defence of a shelter during the breeding phase. Mixed strategies also exist, for example in the genus *Geophagus* from Brazil, where both substrate spawning and mouthbrooding are used. In *G. jurupari* pair first spawns on a rock or hard surface, after which the larvae will be taken up into the mouth by one parent for mouthbrooding (Reid and Atz 1958; Lowe-McConnell 1969). The fry will then be transferred to the other parent as in the examples described for other biparental mouthbrooders. In most other species, a pair will guard a flat rock surface, a cleared patch of sand or gravel, a leaf, a crevice, or a burrow, and they will clean and defend the area for a period prior to spawning (Perrone and Zaret 1979; Kuwamura 1986). The female will attach her eggs to the substrate, at which point they will be fertilised by the male (see Balshine and Abate 2021). After spawning, the pair or a single parent will guard the fry while they remain within the territory. Alternatively, as in the case of the world's largest cichlid, *Boulengerochromis microlepis*, parents may defend their mobile offspring for over a year. In the latter species parents have been sighted with juveniles approaching 10 cm in length (Büscher pers. comm.). This relationship has been suggested to reduce the feeding rate of parental *B. microlepis* to such a degree that death of the parents through starvation might sometimes occur (Konings 2015), though no formal evidence has been gathered on this conjecture.

Fig. 4 Substrate spawning in cichlids. (**a**) *Neolamprologus caudopunctatus* defend a large swarm of fry, (**b**) the black adult *Varibilichromis moori* defends its bright yellow offspring, (**c**) a female *N. multifasciatus* cautiously watches as *Lamprologus callipterus* forages near her territory (photo by Jakob Guebel) (**d**) tiny juvenile *Lepidiolamprologus attenuatus* within a shell, (**e**) a pair of *N. caudopunctatus* perform head down threat displays, potentially to signal danger to their fry (hidden in cave) or ward off potential predators (all photos Alex Jordan)

2.4   Social Group Demography and Dominance Hierarchies

For most cichlids, there is a simple division in social states. While not breeding, they exist as solitary, free-ranging individuals, or they form schools or loose shoals. During breeding, pairs, harems, leks, or colonies may form, during which time social interactions (Fig. 5) with neighbours, rivals, mates, and potential mates may be more frequent and for a time, iterated, which creates opportunities for sexual selection, e.g. in *L. callipterus* (Taborsky et al. 2018). However, these groups are not stable and membership changes frequently, preventing the formation of long-term social relationships.
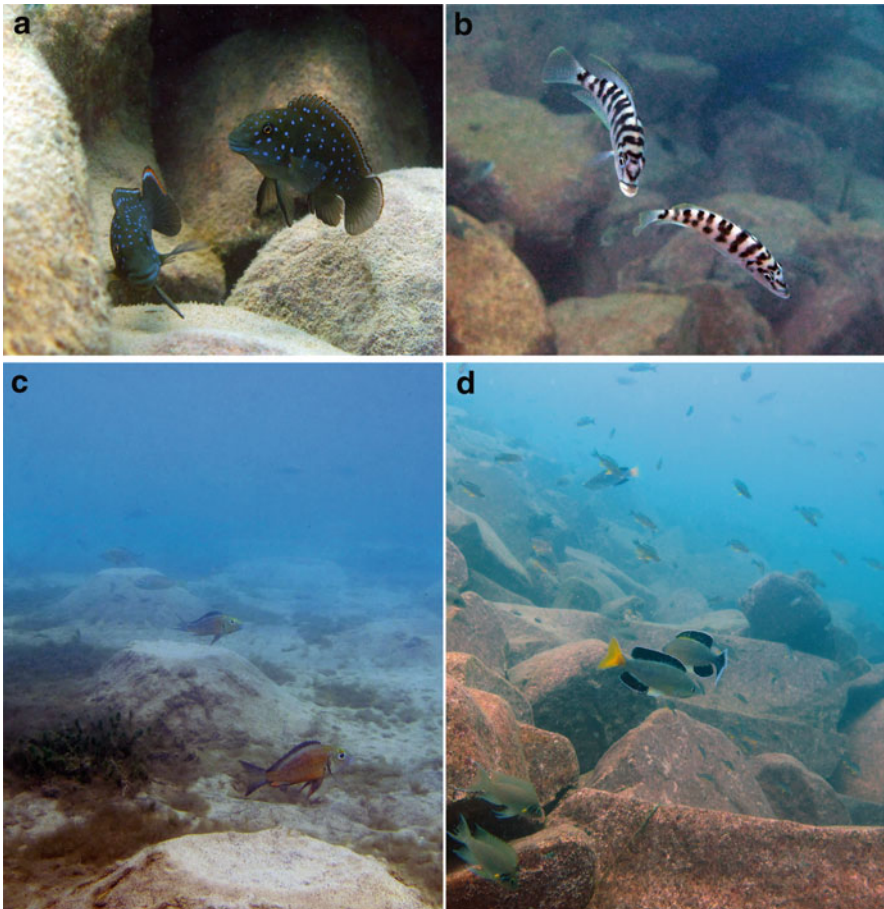

Fig. 5 Social interactions are ubiquitous among cichlids. (**a**) a pair of *Eretmodus cyanosticus* displays in shallow water, (**b**) *Altolamprologus fasciatus* form long-term stable bonds, (**c**) male *Callochromis macrops* display to one another atop their breeding cones, (**d**) male *Cyprichromis coloratus* display to one another by circling with erect fins (all photos by Alex Jordan)

In contrast, some species of cichlids form long-term social groups. When examining group structure, demography, behaviour, and social relationships, one of the best studied species among vertebrates is *N. pulcher* (Taborsky 2016b). The northern phenotype of this species has been originally described as *N. brichardi*, but DNA sequence data suggested merging these populations into one species (Duftner et al. 2007). These fish belong to the Lake Tanganyikan Lamprologines, a tribe containing species with many of the most varied social arrangements of cichlids, or arguably any vertebrate group. In *N. pulcher*, social units typically consist of a dominant pair of breeders and on average between five and six subordinate individuals of various sizes (Taborsky and Limberger 1981; Balshine et al. 2001), known as 'helpers' due to their aid in maintenance, territory defence, and brood care of juveniles to which they may or may not be related (Taborsky 1984; Dierkes et al. 2005). The number of helpers within a group may vary as a function of local ecological conditions; in the north of the lake, there is a small proportion of groups without helpers (~5%), whereas in the south of the lake breeding units lacking helpers are extremely rare (Taborsky and Limberger 1981; Heg et al. 2005b). These differences in demography and social complexity within groups are likely driven by predation risk and the associated benefits of having groups with multiple helpers (Heg et al. 2004a; Groenewoud et al. 2016). In *N. pulcher*, breeder males often move between and defend multiple 'groups' or harems of females and subordinate helpers, in which the males move between groups but females and juveniles do not (Limberger 1983; Desjardins et al. 2008; Wong et al. 2012; Jungwirth et al. 2016). These groups frequently occur in larger colonies consisting of anywhere from a few groups to several hundred (Heg et al. 2008). In other, closely related species such as the rock and shell-dwelling Lamprologines, family structure is similar in that juveniles are frequently found in long-term association with breeding pairs, e.g. in *N. savoryi* (Heg et al. 2005a), *N. obscurus* (Tanaka et al. 2015) and *Julidochromis ornatus* (Heg and Bachar 2006; Awata et al. 2010), but in no other species is the behavioural interaction among individuals as well characterised as in *N. pulcher*.

Within groups of *N. pulcher* there is a strict dominance hierarchy based on body size (Dey et al. 2013). This species has indeterminate growth and is long-lived for its size (up to 8 years in the field, and over 10 years in the aquarium (Jungwirth et al. 2020), but growth rate depends on social rank, group composition, and probably also on cooperative effort, which is energetically costly (Taborsky 1984; Grantner and Taborsky 1998; Taborsky and Grantner 1998; Riebli et al. 2012). Like in most cichlids, size is the primary predictor of contest outcomes, with larger individuals assuming higher positions in the social hierarchies within groups of *N. pulcher* and other species (Hamilton et al. 2005; Jordan et al. 2010a, b; Reddon et al. 2011b; Dey et al. 2013). Similarly, in *Astatotilapia burtoni* the dynamics of social interactions have been well studied, with larger males more likely to win in aggressive contests, and the transition from dominant to subordinate status in this species being characterised thoroughly in both behavioural and physiological studies (Maruska 2015). Differences in size and growth rate may maintain boundaries between social positions in cichlids (Heg 2010), potentially facilitating social niche specialisation (Bergmüller and Taborsky 2007). The presence of multiple age and size classes

within groups may also reduce conflict among members, which may lead to the formation of larger groups (Bergmüller and Taborsky 2010). Because cichlids have indeterminate growth, these size differences persist rather than converging on a single maximum adult size, maintaining the capacity for a group to support different social niches. In *N. pulcher*, the differentiation of social roles, for instance, starts in the earliest life stages at an age of only a few weeks (Kasper et al. 2017). The process of behavioural differentiation probably develops from small asymmetries arising among siblings of a brood over time, resulting in individuals taking up different roles within a social group, thereby reducing direct competition between them (Bergmüller and Taborsky 2010).

2.5   Cooperation

Cooperation is one of the most complex forms of social behaviour, encompassing group hunting, cooperative reproduction, and group defence (Dugatkin 2002). During these group behaviours, individuals may appear to forgo their own selfish interests in favour of actions that benefit the group, but on closer inspection group behaviours are typically explicable from the direct fitness benefits accrued to the individual (Clutton-Brock 2009). Cooperative breeding is less straightforward to explain, especially in contexts where relatedness is low. Why would an individual forgo its own reproduction to aid the rearing of juveniles to whom it is barely related?

Cichlids provide a wealth of insight into cooperative breeding. This process is characterised by the joint care of young produced primarily by dominant group members and is widespread in animals, including invertebrates, birds, and mammals (Brown 1983; Stacey and Koenig 1990; Solomon and French 1997). Cooperative breeding is primarily explained by the fact that when groups have high within-group relatedness, aiding the reproduction of others in the group accrues benefits through inclusive fitness (Hamilton 1964; Griffin and West 2003; Bourke 2011). However, in cichlids and other fish, the generally lower relatedness within fish groups precludes inclusive fitness as an explanation for cooperative breeding. Within fish, cooperative breeding has been described in roughly 25 species of cichlids and a few other species (Taborsky 1994; Heg and Bachar 2006). Like many other advanced social behaviours, cooperative breeding occurs primarily among the cichlids from Lake Tanganyika, where about one-third of biparental substrate brooders in this lake breed cooperatively (Taborsky 1994; Heg and Bachar 2006).

The behaviours involved in cooperation are varied and explained in detail in Sect. 3, but centre around the need to both defend the young and defend and maintain the breeding shelter and territory (Taborsky 2016b). The trade-offs for these cooperative behaviours are significant—helpers grow more slowly than individuals living outside of reproductive groups, due both to their subordinate status within the group (Taborsky 1984; Heg et al. 2004b) and the time and energetic costs of helping behaviours such as digging and defence (Grantner and Taborsky 1998; Taborsky

and Grantner 1998). By restraining growth, helpers can accrue resources to later boost growth after leaving the territory. Most importantly, helpers benefit through increased survivorship in established groups via access to safe shelter sites and larger groups having higher persistence and offering greater protection from predation (Taborsky 1984; Heg et al. 2004b, 2005a). In fact, the benefits of living in groups are apparently so high in this species that almost no individuals live singly in the south of the lake (Stiver et al. 2004). When given a choice, solitary individuals prefer to join groups composed of larger individuals, which offer the greatest potential protection from predation (e.g. Fig. 6), even though by doing so they accept a lower social rank (Jordan et al. 2010b).

The benefits for subordinates to live in groups do not explain why they engage in costly alloparental care. Why not just reap the benefits of group life without investing in the care of others' offspring? This might be explained by group augmentation benefits, as larger groups provide more safety (Heg et al. 2004b, 2005a) and if helpers protect offspring, irrespective of their origin, they may augment the group size for better protection (Kingma et al. 2014). Nonetheless, in *N. pulcher* the apparently most important cause of the helpers' altruistic brood care behaviour is the reciprocal trading of the subordinates' brood care against the benefits they gain from dominants by protection and resource access (Quinones et al. 2016). In other words, subordinates pay rent to be allowed to stay (Fig. 7) in a dominant's territory (Taborsky 1985; Bergmüller and Taborsky 2005; Bruintjes and Taborsky 2008; Fischer et al. 2014). Interestingly, this can render greater fitness benefits to subordinates than helping kin (Jungwirth and Taborsky 2015). In accordance with this, unrelated helpers show higher helping levels than related ones (Stiver et al. 2005; Zoettl et al. 2013b; Quinones et al. 2016), and within groups, helpers may specialise in performing different duties according to their body size (Bruintjes and Taborsky 2011).

3 Behavioural Complexity

From courtship displays and pair-bond reinforcement, social group dominance, submission, and affiliation displays, to communication of danger from parent to offspring, cichlid social communication encompasses a massive range of contexts, information types, and behavioural mechanisms. It was the wealth of behaviours observed in captive cichlids that captured the attention of the early researchers like Noble and Curtis (1939), Baerends and Barends-van Roon (1950), and El-Zarka (1956), who created ethograms rivalling those of mammals in their complexity and behavioural sophistication. Next, we explore a range of contexts and modalities in which cichlids are known to exchange information through behavioural signals.
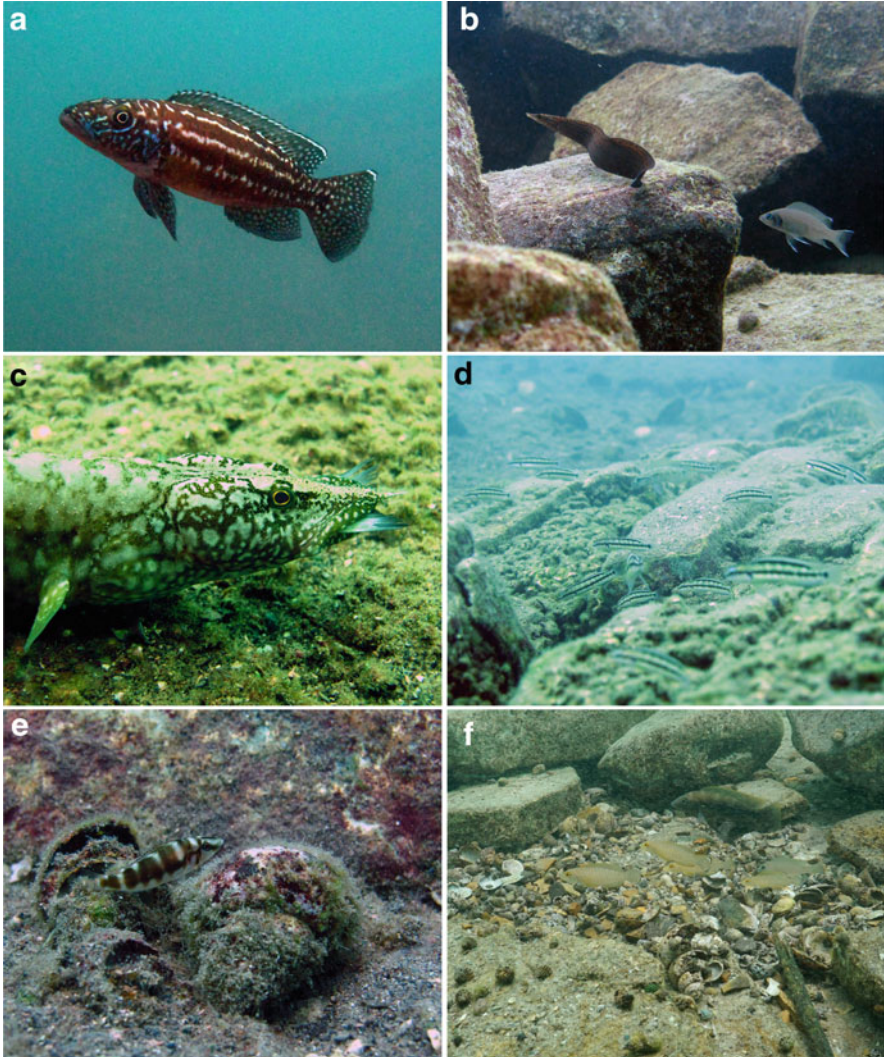
Fig. 6 Cichlids often form social groups to increase protection against predation, which comes in many forms. (**a**) a 20 cm *Lepidiolamprologus kendalli* is fully capable of preying on adults of other species, (**b**) *N. pulcher* chases a *Mastacembalid* eel out of its territory, (**c**) a large *Mastacembalus frenatus* eats a large cichlid prey, (**d**) small *Telmatochromis vittatus* prey on eggs within the nests of social cichlids, (**e**) laterally compressed *Altolamprologus* species are efficient hunters of fry of other species, (**f**) even social groups have trouble defending against marauding bands of *L. callipterus*, which can overwhelm the defence of territory holders, here *L. tetracanthus* (all photos by Alex Jordan)
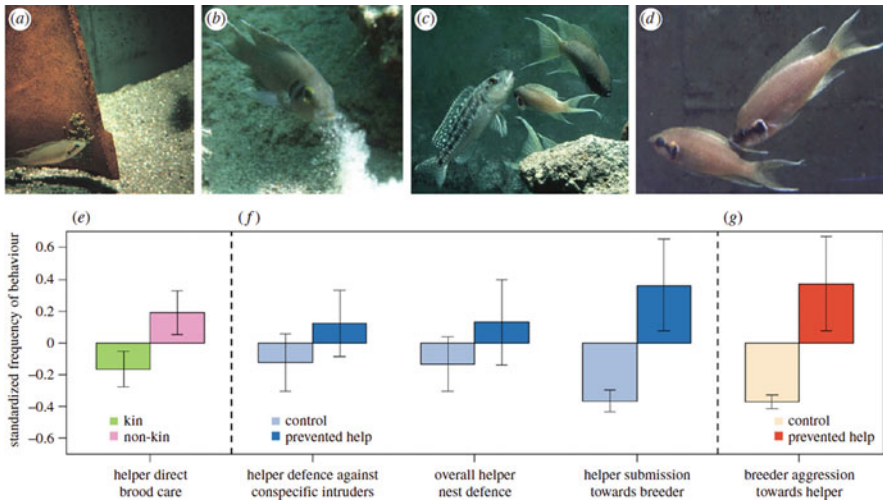
Fig. 7 Cooperative and aggressive behaviours of *N. pulcher* reflect a 'pay-to-stay' mechanism, by which subordinate helpers pay rent for being tolerated in the territory of dominant breeders. Helpers show brood care by cleaning the eggs of breeders (**a**), by performing nest maintenance such as digging out sand from shelters (**b**), and by defending the territory against predators, such as *Lepidiolamprologus elongatus* (**c**). These helping behaviours are prompted by aggression from the breeders. In (**d**), a breeder (right) shows aggression towards a subordinate, and the subordinate responds with submissive behaviour (tail quiver). Panels (**e–g**) summarise the results of experimental manipulations from several studies. Bars show the mean of the standardised frequency of behaviour, with error bars denoting the standard error of the standardised behaviour frequencies. (**e**) Unrelated helpers (purple) provide more help than related ones (green; Zöttl et al. 2013). (**f**) After subordinates have been prevented from giving help (dark blue), they compensate by increasing their previous help and submission level (light blue), presumably in an attempt to appease the breeder (Bergmüller & Taborsky 2005; Fischer et al. 2014). (**g**) Aggression levels in the group are normally very low (cream), but they increase considerably when subordinates are experimentally prevented from helping (red; Fischer et al. 2014; from Quinones et al. 2016)

3.1 Social Interactions Generate Selection for Behavioural Complexity

For a great many group-living animals, social information conveyed among individuals is simple and driven by cues rather than directed signals that have evolved as a mode of communication. An example is the escape response within a group of animals, which can spread among a group by relatively straightforward social contagion of a retreat response in one or a subset of individuals rather than through a complex communication such as vocalisation or other signalling (Krause et al. 2002; Ward and Webster 2016). Importantly in this case, although the cue does communicate information to social partners, the retreat behaviour itself has evolved to avoid predation rather than to communicate to other individuals that danger is nearby. Nevertheless, the escape response may still be used as a source of social information about the presence of predators or the level of risk.

Avoiding predation is the primary functional explanation for group formation in many species (Pitcher 1986) including largely anonymous, collective behavioural processes that do not rely on complex signalling (Treherne and Foster 1981). In the wild, cichlid communities are dense and composed of numerous social groups and different species (Rossiter 1995). A rapid retreat response from one individual of any species in these groups can promptly propagate throughout a community, especially in shell-dwelling communities (A Jordan pers. obs.). Similarly, producer-scrounger feeding aggregations may form through social cues, with some group members waiting for others to find a food item or patch and using that social information to move in and begin feeding themselves (Giraldeau and Caraco 2018). This is the common feeding mode of *L. callipterus*, which use social information to detect and exploit rich food patches in a producer-scrounger situation. Again, the cue leading to information spread within the group, feeding behaviour, has not evolved for the purpose of communication. The key point is that although these mechanisms can provide information to members of a group, they have not evolved as signals and do not require specialised behaviour to communicate information.

It is when more complex types of information must be passed among individuals that the stage is set for selection to produce more advanced communication behaviours. This is especially true when the identity of signaller and receiver interact to modulate the meaning and salience of information, providing further selective pressure on socio-cognitive capacities and increased behavioural sophistication. Hierarchy in particular can be a powerful mediator of social behaviour, affecting the nature and frequency of interactions (Rodriguez-Santiago et al. 2020), as well as social (King et al. 2008) and collective movement decisions (Nagy et al. 2010). Indeed, when studying animals living in groups, it is always necessary to consider the effect of social influence on the behavioural output of any one individual. In groups of the shell-dwelling cichlid *N. multifasciatus,* for example a behavioural change in one individual can rapidly spread through the group, changing the overall social structure of the group as a function of an initial behavioural change in only one member (Jordan et al. 2016). Perhaps because of this interdependence within their groups, communication in social cichlids has developed into some of the richest and most sophisticated in the animal world.

3.2   Communication Modalities

A major question in cichlid research has been the adaptation of sensory and signalling systems to prevailing environmental conditions. In particular, much research effort has concentrated on the evolution of colour diversity in response to the light environment and how this process has affected the African cichlid radiation (Seehausen et al. 1999, 2008). More generally, the communication modality that has received far and away from the greatest research attention in cichlids is the visual system (Korzan and Fernald 2007; Chen and Fernald 2011), a research trend common for most fish species (Rosenthal and Ryan 2000) that we explore in greater

depth below. However, just as for other fish, cichlids also incorporate auditory (Amorim et al. 2003, 2008, 2015; Miguel Simões et al. 2008; Maruska and Fernald 2012), chemosensory (Barata et al. 2007; Keller-Costa et al. 2015; Bayani et al. 2017), and mechanosensory communication (Butler and Maruska 2015) in their social interactions.

In cichlids, 29 species have been described as sound producers (Longrie et al. 2013). Auditory communication has been examined primarily in the context of the physiological mechanisms underlying hearing and sound production, a logical trend given the long and successful history of morphological comparative studies in cichlids. Swimbladder and ear morphology have been compared within cichlids and in comparison to non-cichlids (Braun and Grande 2008; Schulz-Mirbach et al. 2012; Ladich 2016) and behavioural studies have demonstrated the role of auditory communication among cichlids, for example during courtship displays (see Lobel et al. 2021). In *Oreochromis mossambicus* both male–male contests and male–female courtship are accompanied by sound production (Amorim et al. 2003). Similarly, in *A. burtoni* males produce sound during their courtship display, and females prefer to associate with males when the presentation of these males is accompanied by courtship sounds compared to noise controls (Maruska and Fernald 2012). These sounds, which often are produced through chewing or body vibration (Longrie et al. 2013), seem to play a role in social communication. Yet we are at a relatively early stage in our understanding of the context in which these signals are produced and their effect on the behaviour or the recipient.

Chemosensory and olfactory communication play a major role in aquatic environments and are known to be important in social affiliation also in other freshwater species such as stickleback (Ward and Hart 2003). In cichlids, this sensory modality is also used in numerous social behavioural contexts. Both courtship and aggressive contests may involve increased rates of urination prior to and during interactions, and the urine composition may be modified according to the social context (Hirschenhauser et al. 2008). For instance, the urine of dominant males may contain higher concentrations of chemical cues than that of subordinate males (Miranda et al. 2005; Barata et al. 2007). Indeed, urination during contests may be a direct form of signalling to rivals, as suggested in *N. pulcher* where aggressive propensity is communicated via urine-borne chemical compounds (Bayani et al. 2017). Morevoer, chemical cues are importantly involved in recognition mechanisms, for instance, in kin recognition of *N. pulcher* (Le Vin et al. 2010).

Cichlid social communication also appears to rely on the mechanosensory system (see Webb et al. 2021), the role of which has recently been examined in contest behaviour in *A. burtoni* and discussed in general terms by Butler and Maruska (2015). Since the early studies of Baerends it has been noted that cichlids perform behaviours such as 'tail-beating' during male–male agonistic encounters, and during these behaviours the physical displacement of water may provide a signal of the opponent's size or strength (Baerends and Baerends-van Roon 1950). By ablating the lateral line system, and thereby disrupting the mechanosensory system, Butler and Maruska (2015) provided evidence that detection of these water-borne

vibrations is necessary for contest resolution in *A. burtoni*, demonstrating that this modality may be required for effective resolution of social conflicts.

3.3 Aggressive/Agonistic/Territorial Interactions in Cichlids

Such is their willingness to engage in territorial disputes that cichlids are notorious among aquarium hobbyists for their quarrelsome nature. Many a pet store purchase has ended in disaster when too many, or too few, cichlids are housed in aquaria. Of course, this behaviour is not restricted to captivity; in their natural habitat territoriality and aggressive behaviours are some of the most commonly observed in wild cichlids. The form and expression of aggressive behaviour in cichlids are highly conserved across species and involves stereotypical interactions that progress through clear stages of escalation. Two males engaged in a territorial dispute will generally initiate disputes with a frontal display with the head pointing downward and the opercula, branchiostegal membrane, and fins spread. Upon escalation, the males may proceed to fast approach, tail-beating, circling, chasing, butting, biting, and mouth-fighting as the conflict intensity increases. Baerends and Baerends-van Roon (1950) divide territorial and aggressive behaviour into three different categories: chasing, intraterritorial fighting, and boundary fighting. 'Boundary fighting' involves a series of stereotyped signals and colour changes to signal to any potential intruders, but may also be used in interactions with neighbours and rivals. Typically, the resident will face towards the intruder with fins spread and may perform a jerking swimming pattern. The opercula may then be spread and the pair may engage in back and forth swimming behaviour such that the advance of one individual is met with a retreat by the other, and then vice-versa. Early researchers interpreted this behaviour in stickleback as a compromise between aggression and fear, each being represented behaviourally in turn (Leiner 1929). If the boundary is breached, response to territorial incursion involves lateral displays in which the medial fins are erected and the branchiostegal membrane extended. This is associated with exaggerated swimming toward the intruder, potentially providing a mechanosensory signal. This 'intraterritorial fighting' will be escalated if the intruder does not leave, at which point overt butting and biting of the flanks will occur. If the intruder reciprocates this behaviour, the pair will engage in continuous circling behaviour in which each attempt to perform lateral rams and bites towards the other, or opponents will lock their jaws and try to push or turn the body of the opponent, until one performs submissive behaviour and leaves the territory. Once this dominance has been established, 'chasing' behaviour may occur. As the name implies, chasing constitutes a directed aggressive act from a socially dominant individual toward a fleeing subordinate individual, typically as a mechanism to further remove an intruder from a territory, and may include attempts at physical damage through biting during the chase. Aggressive displays or behaviour may also be responded to with submissive behaviours, which may themselves be diverse and nuanced, but on which little empirical work has been conducted. Engaging in physical contests can be costly

because rivals expend energy and time, risk injuring themselves (Briffa and Sneddon 2007), and especially in high predation environments like Lake Tanganyika, may increase exposure to predation through the reduction in attention (A. Jordan pers. obs.). As such, memorising dominance relationships and performing submissive behaviour rather than reciprocal aggression can be adaptive by reducing the costs of unwinnable contests (Barnard and Burk 1979).

As discussed earlier, resource defensibility is a key factor in determining social behaviour and territoriality in animals (Brown 1964), and has a particularly strong effect on antagonistic interactions in cichlids. This effect can operate on two levels and timescales—it can lead to fixed among species differences and labile within species differences. This latter effect is exemplified in the transition from free-ranging, non-aggressive, and shoaling behavioural phenotypes during non-breeding periods to the highly aggressive and territorial behaviour displayed by the very same individuals during breeding. In *Oreochromis mossambicus*, the distribution of male territories shifts from non-uniform ranges with flexible boundaries in non-breeding states to highly ordered and uniform territory ranges once all males enter breeding condition (Barlow 1974a, b). This change in territory packing is a consequence of the shift in aggressive behaviour towards other males and has consequences on the social and spatial structure of the population generally (Chase and Seitz 2011). In many other species of cichlids, the change from a non-breeding to a breeding state is accompanied by massive increase in territoriality and aggression. The mechanisms underlying this behavioural transition are well understood, particularly in the African riverine mouthbrooder *A. burtoni*, where social status changes are associated with a range of gene expression, endocrine, and morphological shifts. The details of the mechanisms underlying these social changes are discussed by Félix and Oliveira (2021).

3.4 Courtship and Mating

Here we discuss the range of communication and behaviour expressed during reproduction, which is by definition a social act. As in all taxa, there is a great difference in the behaviour of species that first form pairs, harems, or cooperative groups prior to breeding, and those which come together only in the act of courtship and mating itself. In pair-bond forming species, reproduction, and cohabitation may involve almost the entire behavioural repertoire, while in those species that only couple during mating, lekking, and male courtship are the most common behaviours (Schuetz et al. 2010; Haesler et al. 2011; Schütz et al. 2017). The majority of teleost parental care systems, male-only (paternal) brood care is extremely rare in cichlids, which has important ramifications for the operational sex ratio and mating behaviour. Primarily it means that female choice for male ornaments and courtship is more common where paternal investment after copulation is low because the operational sex ratio is biased towards a greater number of males who must compete for mating opportunities. In Haplochromines, for instance, where males form temporary leks

and eggs are incubated by the female, sexual dimorphism is far more pronounced than in pair-bonding and group breeding species, where sexes may closely resemble one another. In *L. callipterus*, the sexual size dimorphism has reached its extreme, with males outsizing females on average 12 times by weight, which is the greatest sexual dimorphism known among animals with males exceeding females in size (Schütz and Taborsky 2000, 2005). Interestingly, in this species there is also an extreme intrasexual dimorphism between large, bourgeois nest building males and tiny reproductive parasites, which reach only 2.5% of the mass of nest males (Sato et al. 2004). This intrasexual size dimorphism is fixed for life, representing a sex-linked Mendelian single locus genetic polymorphism. The dwarf males in this species do not court, but surreptitiously enter the territory of a nesting male to fertilise a large proportion of the deposited eggs using highly specialised behavioural and gametic traits (Taborsky 2001; Wirtz-Ocana et al. 2013; Ocana et al. 2014).

In species without post-zygotic paternal care, males typically first choose a site from which to court passing females. This may be a flat stone, a patch of gravel cleared of debris, or a purpose-built bower constructed from sand. These structures can be discrete, like in *O. ventralis*, where only a thin layer of fine sand is deposited on a horizontal stone surface (Immler and Taborsky 2009); but they may alternatively be impressive in their construction, like in the bower building cichlids of Lake Malawi and Lake Tanganyika (McKaye et al. 1990; Schaedelin and Taborsky 2006). In *Cyathopharynx furcifer*, for instance, a fish only 15 cm in length, males construct sand craters of more than 40 cm in diameter, moving on average over 5 ½ kg of sand and spending 80% of their time transporting sand when constructing these craters, mouthful per mouthful (Schaedelin and Taborsky 2006). On average, the males expend 18 hours net building time to complete such crater, which involves a total swimming distance of >8 km for transporting the required amount of sand (Bucher 2004). Each male builds a crater matching in size to his own competitive power. Females assess males according to their individual crater building activity. These elaborate sand structures exemplify individual-specific extended phenotypes that are evaluated by females during mate choice (Schaedelin and Taborsky 2009).

In general, if males monopolise spawning sites they tend them carefully and defend them vigorously against conspecific rivals and heterospecifics while waiting for passing females. Such territory can take many forms, from a depression in the sand as in many Tilapia type species, a constructed bower as in many Tanganyika Ectodines (see above), or simply a volume of water defended against other males as in some *Cyprychromini*. When a female is nearby, males dart out rapidly from their territory and perform a series of fin extensions, quivering, and body arching towards the female, attempting to entice her back to their territory. If the female shows interest, the male will repeatedly attempt to lead her, swimming in front of the female with quick and exaggerated swimming movements oriented towards their spawning site. Arriving at the spawning place, the male and female may engage in repeated circling, which is the time when gametes are released and taken up into the mouth of the caring parent. In many species the male will then present its egg dummies with quivering body movements. Egg dummies are brightly coloured spots or tassels that somewhat resemble the species eggs. They can be positioned either on the anal fin

and also on the dorsal fin or on extended filaments of their pelvic fins (Wickler 1962; Hert 1989; Salzburger et al. 2007). Responsive females will touch the dummies with their mouth as if attempting to take them up. This is probably the moment when they collect the sperm that males deposit on the bottom of their spawning site (Immler and Taborsky 2009). In *O.ventralis*, the eggs are fertilised in the mouth of the female, and she usually collects several ejaculates from different males in a sequence. This provides opportunities for post-mating sexual selection to take effect, as sperm compete for fertilisation in the female's mouth without the direct influence of their producer. The owner of the bower is therefore not necessarily the father of the resulting offspring (Immler and Taborsky 2009; Haesler et al. 2011).

Typically, in lekking mouthbrooders, the social interactions encompassing the male-female pairing are brief—a transient sexual relationship is formed immediately prior to fertilisation of the eggs, during which aggression from the male is reduced. Once fertilisation is complete however, the female is often chased vigorously from the territory (Seitz 1940). Hence, the social system in many mouthbrooding cichlids is rather simple, with interactions among adults confined to territorial aggression among males and the brief interaction between male and female during gamete deposition and uptake. For pair-bonded, haremic, and social species, the process of courtship and mating is more nuanced and long-term, and is associated up with the process of social behaviour and territory defence more generally. Often, the pair-bond will form long before the act of spawning, and may begin with one or both sexes constructing, cleaning out, or defending a permanent or semi-permanent territory. Courtship itself may be similar to that of mouthbrooders with only temporary associations, with a series of fin extensions, quivers, and leading behaviours prior to spawning. Nevertheless, there are species-specific sequences and structures of behaviour that offer a fascinating window into the evolution of courtship itself, as well as being potential pre-zygotic barriers to hybridisation. While the details of parental care in cichlids are dealt with elsewhere in this volume, it is during and after this phase that many other types of social interaction are also displayed. Between the members of the pair, behaviours that resemble aggression, but which are performed at a slower speed or in a constrained fashion are common. Affiliative behaviours such as 'hook swimming' and 'soft-touch' (Sopinka et al. 2009) are often performed by subordinates towards dominants, or by females towards males. These forms of display are often performed after the return of one individual from territorial defence or having briefly left the territory, and may function as a form of pair reinforcement. As for other social signals, there is considerable variation among species in the form and function of these affiliative and submissive behaviours, and uncovering the causes and consequences of this variation offer much scope for future research. Finally, reproductive behaviours themselves may be used as a subtle social signal to deceive or manipulate partners. In *Julidochromis spp*. females may perform 'pseudospawning' behaviour, a behaviour frequently shown by many cichlids preparing for the synchronous release of gametes during spawning. This behaviour of *Julidochromis* females was interpreted as 'pretending' to lay eggs along the substrate to confuse males regarding the number of offspring they have actually sired with that female, and thus providing more paternal effort and defence toward her brood

(Kohda et al. 2009). This is reminiscent of the situation in dunnocks, a small songbird with similar polyandrous mating patterns, where females solicit matings with group males differing in rank, which may increase the propensity of males to care for the brood (Davies et al. 1996).

3.5 Signalling Danger (Predation)

Cichlid parents are highly attentive and may provide care long into the development of their offspring. This is often provided within the spawning territory of the parents, where the fry are afforded some degree of protection from predation. As the cloud of fry ascends from the substrate in order to feed, one parent, both parents, or in the case of cooperative breeders, parents and helpers will remain vigilant for approaching predators. If a threat is detected, the parents will quickly signal to the fry using, for instance, a series of fin flicks and subtle body movements. One of the most used signals is an abrupt raising and lowering of the dorsal and pectoral fins, which Liebig (1920) described in *Cichlasoma biocellatum* as serving to either attract or repel the fry, depending on the speed of the motion. The same behaviour in *H. bimaculatus* was interpreted by Fischer (1924) as a signal to attract young to food sources, and subsequent authors studying *Nannacara taenia* (Stoye 1933) and *Aequidens latifrons* (Breder 1934) interpreted these purely as warning signals to the fry, which would rapidly descend to the substrate. Other species will take offspring back into the mouth if a dangerous predator appears after the initial release in a process described as iterocavous mouthbrooding. Examples of this strategy include species within the South American *Geophagus steindachneri*, the African cichlids *Pseudocrenilabrus multicolour* and the *Tropheini*. These species rapidly take fry into their buccal cavity at the sign of danger or will signal to fry using pelvic fins and head down posture, at which point fry rapidly swim back into the mouth.

3.6 Helping and Cooperation

Intra-group social communication is best studied in cooperatively breeding cichlids, where different group members may assume divergent roles, depending on size, status, and sex. A variety of potentially sex-specific (Mitchell et al. 2009) aggressive, affiliative, and submissive behaviours are involved in the establishment and maintenance of dominance relationships among group members (Taborsky 1984; Hamilton et al. 2005; Dey et al. 2013). Sex can also affect dominance acquisition among same-size subordinates (Riebli et al. 2012), and growth patterns (Hamilton and Heg 2007). Cooperative behaviours in such groups often involve keeping predators at bay by aggressive defence behaviour (Fig. 3c), providing shelters (e.g. by digging out cavities under stones that can serve for breeding; Fig. 3b), cleaning eggs and larvae with the mouth (Figs. 2b, 3b), and fanning eggs for oxygen

supply. Tasks may be shared unequally between group members, depending on current demands (Taborsky and Limberger 1981; Taborsky 1984; Desjardins et al. 2008). In the cooperative breeder *N. pulcher*, if several demands appear concurrently, helpers may specialise in territory maintenance, whereas female breeders focus on direct brood care and both breeders heavily engage in defence (Taborsky et al. 1986). Large, piscivorous predators are attacked most often by male breeders, followed by female breeders and large helpers. Defence against dangerous predators is often shared and strategic risk sharing among group members is suggested by significant positive correlations between group size and the per capita attack frequencies of breeders and large helpers against experimentally deployed large predators (Heg and Taborsky 2010). Among helpers, large individuals may either specialise in defence behaviour (Taborsky and Limberger 1981) or in digging while smaller helpers defend the breeding shelter against egg predators (Bruintjes and Taborsky 2011), depending on ecological challenges and the negotiation process between breeders and helpers (Naef and Taborsky 2020). When helper-sized fish cooperatively dig out a common shelter, they apparently apply direct reciprocity decision rules to decide about their digging effort (Taborsky and Riebli 2020).

In this species, social behaviours such as aggression and submission among group members make up the bulk of the behavioural time budgets of both breeders and helpers, with aggression and submission dominating the time and energy budgets of breeders and helpers, respectively (Taborsky and Grantner 1998). Among the cooperative behaviours, territory maintenance takes up a considerable proportion of the behavioural time budget of helpers and female breeders. In addition to digging, territory maintenance also includes the removal of stones, shells, and particles as well as cleaning the spawning site. The energetic investment of territory maintenance involves a six-fold increase of energy expenditure compared to the routine metabolic rate, which is comparable to the energetic costs of flying in birds (Grantner and Taborsky 1998). During breeding, digging is responsible for nearly 20% and 25% of behavioural metabolic costs in helpers and female breeders, respectively, with expenses varying among different stages of the breeding cycle (Taborsky and Grantner 1998).

4   Cichlids as a Model for Studying Social Behaviour

Understanding the ecological and evolutionary pathways leading to social behaviour is a long-standing challenge in biology. A major difficulty lies in isolating the sources of selection that may favour the evolution of particular social systems, especially when comparisons are confounded by variation across ecological, geographical, or life-history parameters. The controversy around the social-brain-hypothesis reveals the difficulties in associating variation in a putative mechanism of complex sociality (brain size) with one or other causative factor, in this case group size or dietary breadth (DeCasien et al. 2017; Powell et al. 2017). Ideally, we would have a system in which there is variation in the trait, or traits of interest, with minimal

variation in other potentially confounding factors. When considering social evolution and social behaviour, cichlids—and in particular Lake Tanganyikan Lamprologine cichlids—offer just such a system.

4.1 Phylogeny and the Evolution of Sociality

A major strength of cichlids as a study group is their well-resolved phylogeny, which has been leveraged to understand many aspects of morphological and genomic radiation. Within and across the African Great Lakes (Old World) and Neotropical regions (New World), there is a great diversity of social systems and social behaviour, and since the early work of Baerends and Baerends-van Roon (1950), the utility of comparative behavioural studies in cichlids has been recognised. However, the inherent difficulties of quantifying behaviour at anything approaching the detail and objectivity achieved, for example in morphological studies, have constrained comparative behavioural studies to use broad categories and classifications (e.g. Gonzalez-Voyer et al. 2008). This can limit the resolution of behavioural comparisons and cause disagreement over the categories themselves (Dey et al. 2017; Tanaka et al. 2018a). Of particular importance in this debate, and a major challenge for researchers is the assignment of species into categories of social structure and mating patterns using quantitative, rather than qualitative descriptors (Lein and Jordan 2021).

The primary source of this difficulty is that although cichlids have a dazzling variety of mating patterns, many of these do not fall easily into discrete mating system categories as originally proposed (Emlen and Oring 1977). Moreover, for many species, mating patterns and social arrangement are a function of resource availability and other ecological factors, and variation in social arrangement and behaviour within species living in different locations is commonplace (e.g. Groenewoud et al. 2016). One difficulty in ascribing species-level categories or social descriptors can be found when species themselves are ill-defined, for example in *Telmatochromis temporalis*. Like in many cichlids, the taxonomic status of this species is subject to some disagreement: while the populations on rocks have consistently been described as *T. temporalis* (Sato and Gashagaza 1997; Konings 2015), populations found on shell beds have been described as both the same (Hanssens and Snoeks 2001) or later as different species (Hanssens and Snoeks 2003). Takahashi (2004) describes behavioural and molecular differences between morphs, suggesting they constitute two separate evolutionary lineages, and goes on to demonstrate differences in social structure between the 'normal' and 'dwarf' morph with respect to number of females in a male's territory as a function of body size. Although there is apparent directional selection on larger body size in both morphs through increased access to mates, this is countered in shell-dwelling morphs by the need to enter the shell, leading to their smaller average size (Takahashi and Koblmüller 2011).

This difference between rock and shell-dwelling morphs is not restricted to this species—both *N. pulcher* and *N. multifasciatus* occur in rock and shell-dwelling populations, with distinct, but as yet unquantified, differences in their social arrangements. In the well-studied Kasakalawe population of *N. pulcher*, group territories are clearly separated, inhabiting rock territories interspersed in sand patches (Balshine et al. 2001; Heg et al. 2005b). In contrast, the shell-dwelling *N. pulcher* population at Mwina exists in massive aggregations of hundreds of interacting individuals making it difficult to distinguish social units (A Jordan & M. Taborsky pers. obs.). Similarly in *N. multifasciatus*, the effectively endless availability of shells in the Chikonde population is correlated with very large group sizes of 50 or more individuals, whereas other populations in areas of lower shell abundance (e.g. Mbita Island, Ndole Bay), as well as the rock-dwelling populations, contain many more pairs or polygynous harems (A. Jordan pers. obs.). Other ecological factors can similarly influence social structure; a comparison between populations of *N. pulcher* reveals that social organisation and behaviour is strongly affected by predation risk and associated ecological factors (Groenewoud et al. 2016). In areas with high predation risk, groups more often contained more large than small members, whereas in areas of low predation this trend was reversed. These examples demonstrate that social structure can vary in subtle ways that extend beyond social categories such as asocial, group-living, monogamous, or polygynous. Given our increasing understanding of the fitness consequences of variation in social structures (Ward and Webster 2016), as well as the controversy that can arise over these broad categories, a more standardised and quantitative assessment of variation in social structure is clearly needed. As we outline in the section on future directions, the advent of automated tracking of large groups of cichlids that is now possible may generate far greater insight into the interactions, identities, and social structure of both captive and wild cichlid groups (Lein and Jordan 2021). With robust descriptors of social interactions and group dynamics in quantitative space, differences in both social arrangement and behaviour can be mapped directly onto phylogenies to generate testable hypotheses about social evolution. This in turn will allow us to interrogate what the social, ecological, neurobiological, and physiological pressures and constraints on behaviour may have been over evolutionary time.

A particularly powerful system for studying sociality in cichlids is that of the tribe Lamprologini, which contains species with similar ecological niches, but a breadth of social systems, including almost all cooperatively breeding fish species described to date (Taborsky 1994; Sato and Gashagaza 1997; Heg and Bachar 2006). The diversity in social behaviour among a group of species that shares many other aspects of life history allows for a powerful comparison of the forces shaping behaviour without confounding differences in geography, morphology, and ecology. This is well-represented in the 15 or more 'shell-dwelling' Lamprologine cichlids. Aside from their close phylogenetic relatedness, these dwarf species are also very similar in terms of their ecology. All 15 species known exclusively use fossilised shells of the genus *Neothauma* for shelter from predators and brood chambers; all face similar predators, predominantly from the related genus *Lepidiolamprologus*; all have overlapping dietary niches, although some feed benthically and some from

the water column (Ota et al. 2012); all are morphologically similar (i.e. they are small) as a consequence of needing to be able to enter shells; all practice some level of paternal care by fanning oxygen into the shell thus ventilating the eggs until these hatches and subsequently defending offspring from being eaten; and all occur at similar depth ranges, often on vast shell beds, and many are found syntopically in mosaic communities.

Despite their similar ecological lifestyles, there is a striking divergence between species in terms of the social strategies that are adopted. The species *N. multifasciatus, N. brevis* and *L. ocellatus* exemplify this divergence in the social system, but are members of a much larger group in which comparisons are possible. *N. multifasciatus* is the smallest cichlid species known (m: 30 mm SL, f: 20 mm SL) and lives in depths as shallow as 10 metres on beds of *Neothauma* shells, which it excavates in small funnel-shaped depressions of the sandy lake bed, and which are inhabited by stable social groups of up to 30 or more individuals (typically around 2–3 adult males and 4–5 females; Kohler 1998, Jordan et al. 2016). The second species, *N. brevis* is substantially larger (m: 60 mm SL, f: 40 mm SL) than *N. multifasciatus* and forms temporary breeding pairs that inhabit often only a single shell on the widely shell-scattered open sand habitat. In the similar-sized species *L. ocellatus*, by contrast, large males hold small harems of 2–3 females and defend a territory of approx. 1–3 m^2 in diameter against intruders. Similar to *N. brevis*, theses shells get partially covered with sand (Konings 2015). These three species exemplify the range of social complexity, but there are many other dwarf shell-dwelling Tanganyika cichlids that differ somewhat in their social organisation while maintaining many other aspects of ecology and life history, including *N. multifasciatus, N. similis, N. brevis, N. calliurus, N. pulcher, N. ornatipinnis, L. ocellatus, L. callipterus, L. caudopunctatus, Telmatochromis vittatus, T. temporalis,* and *Lepidiolamprologus meeli* (Sato and Gashagaza 1997).

Variation in social organisation in populations that face similar ecological pressures, such as the shell-dwelling cichlids, provides a powerful comparative system for understanding social evolution but must be combined with an understanding of the behaviours expressed by individuals within the respective social units. We now move on to discuss behaviour at the level of the individual, before examining how an understanding of both social structure and individual behaviour can provide fundamental insight into the evolution of sociality generally.

4.2 Plasticity, Behavioural Development and Individual Differences

While there is an amazing diversity of social behaviours displayed among cichlid species, behavioural expression among individuals can be equally diverse. It has been clear since the concept of selection was introduced by Darwin that consistent variation among individuals is required for behavioural evolution to occur. This

variation is the raw material upon which selection can act. The behaviour may be consistently expressed for shorter or longer periods, and be more- or less-varied among individuals, depending on the mechanistic basis of the behaviour being expressed. Variation in behaviour generally results from an interaction between genetic determination and environmental/social effects reflected in phenotypic plasticity. The relative importance of these sources of variation can greatly differ, ranging from highly conserved, more, or less fixed action patterns with a putative genetic basis such as honeybee cleaning of cells (Oxley et al. 2010), to more complex and highly variable behavioural traits such as observed in social interactions (Chervet et al. 2011), the mechanisms of which remain the focus of much ongoing research.

To date there is only limited evidence of genetic polymorphisms governing differences in cichlid social behaviour, with the prominent exception of alternative male reproductive tactics. The Tanganyikan cichlid *L. callipterus* exhibits two divergent, genetically determined male morphs. Giant males build nests consisting of up to hundreds of empty snail shells, and they court females that lay their eggs inside these shells. Tiny 'dwarf' males sometimes manage to enter a snail shell in which a female is spawning to fertilise eggs from the tip of the shell, thereby parasitizing the effort of the giant nest owners (Taborsky 2001; Sato et al. 2004; von Kuerthy and Taborsky 2016). Only males are affected by this genetic polymorphism, which is inherited via the male Y-chromosome or some other sex-specific genome region (Ocana et al. 2014). Furthermore, the yellow and red male colour morphs of the West African riverine rainbow krib (*Pelvicachromis pulcher*) seem to be genetically determined (Heiligenberg 1965; Martin and Taborsky 1997) and are linked to male mating tactics. Red males always defend a territory holding one or several females, whereas yellow males may either mate monogamously or become 'satellite males' or helpers, which do not have a female partner on their own but help red males in territory defence and brood care while taking a share in siring offspring (Martin and Taborsky 1997).

While these examples of male genetic polymorphisms in morphology and social behaviour are impressive, they might be rare in cichlids (Taborsky 2008). In contrast, individual differences in social behaviour shaped by experience seem far more widespread, with important effects often lasting for life. Phenotypic plasticity refers to the ability of a genotype to express different phenotypes depending on the environmental conditions it experiences and is a specific case of a more general gene-by-environment interaction. It allows organisms to adapt quickly to changes in the environment and thus it may help these organisms to survive rapidly changing conditions. This seems particularly important in the context of social interactions. In general, as plastic adjustments can take effect much faster than evolutionary change, plasticity may rescue populations exposed to changes in their environment before a strategy to cope with a stressor can evolve (Chevin and Lande 2010).

Recently, there has been a rapid increase in our understanding of how the diversity of social behaviour observed in a single cichlid species originates from plasticity. Plasticity can affect social behaviour at two temporal scales; (1) long-term effects, where the social environment a fish experiences during its development

shortly after birth shapes social behaviour irreversibly ('developmental plasticity') and (2) short-term adjustments of the phenotype, which are typically reversible ('flexibility'). Such flexibility is shown, for instance, if the current dominant fish of a social group is temporarily removed and a previously subordinate group member may switch to claiming the dominant status. Once the former dominant fish is reinstalled in its territory, the previous ascender may fully reverse back to a subordinate state. In *A. burtoni* males, switching from a non-aggressive, subordinate state to a dominant hierarchy position is accompanied by a drastic change in behaviour, in which ascended dominants show high aggression against any other male. The behavioural change is accompanied by the expression of a bright colour pattern interspersed with strongly contrasting black stripes and bars (Maruska and Fernald 2018).

Developmental plasticity, however, is more difficult to explain than such fully flexible adjustments, because irreversible changes made early in life have consequences for the entire life including adulthood at a time when the future social conditions cannot be anticipated with certainty. This means that if the environment in which a fish develops is a poor predictor of the future, an individual is bound to live with a somewhat maladapted phenotype. Therefore, the lifelong effects of developmental plasticity should only occur if the future can be predicted with some reliability (Burgess and Marshall 2014). The challenge of studying the effect of developmental plasticity on fitness is that all life stages and environmental conditions encountered during the course of an individual's life have to be considered to test for pleiotropic and other negative effects. Often this is only possible in captive studies under controlled experimental conditions.

The cooperatively breeding cichlid *N. pulcher* is an ideal species to study the developmental plasticity of social behaviour. Its natural habitat in Lake Tanganyika represents a predictable world: group sizes of social units may remain stable over years (Heg et al. 2005a) and, while predation risk differs between separate populations (Groenewoud et al. 2016), it is predictable within populations, where it partly depends both on group size and the distance to neighbouring territories (Jungwirth and Taborsky 2015). In the aquarium, the social environment after birth can be easily manipulated experimentally. This may be done, for instance, by rearing young in groups containing either the parents with or without helpers or the same-aged siblings only (Arnold and Taborsky 2010; Taborsky et al. 2012). Similarly, social complexity in early life can be manipulated by keeping young in large groups with parents and many helpers, or in small groups in which the breeder pair only has one helper (Fischer et al. 2015). In both studies using such experimental variation of rearing conditions, individuals reared in a social setting with more adults and helpers being present were better able to solve contests efficiently later in life and they were more likely accepted as subordinates in a territory by large fish. As such effects persist throughout life (Fischer et al. 2017), this suggests that offspring reared in more complex social environments had developed a better social competence during early life (Taborsky and Oliveira 2012).

Apart from causing quantitative differences in social behaviour, developmental plasticity may also give rise to lifelong behavioural specialisation. As outlined
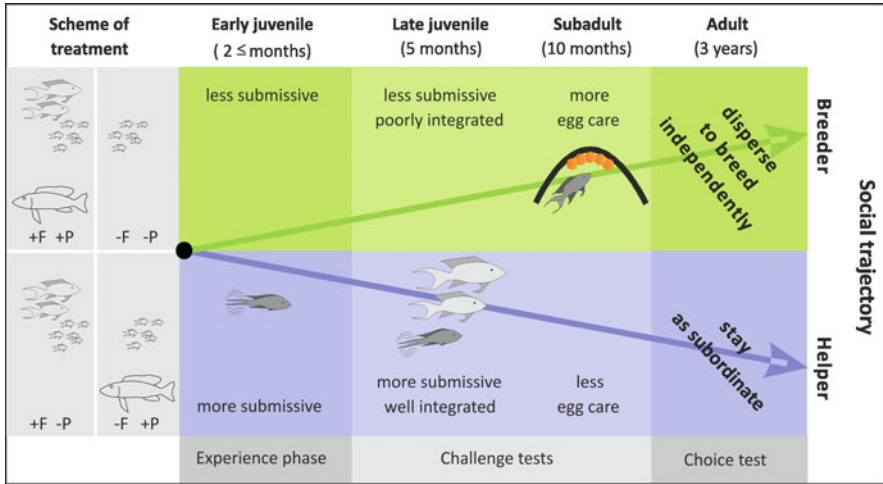
Fig. 8 In *N. pulcher*, the early social environment and predation risk interact to induce a specialisation in one of two social trajectories, (1) individuals that have a higher propensity to act as brood care helper, which disperse early for independent breeding, and (2) individuals that show a higher propensity to exhibit submissive behaviour, which remain philopatric. On the left side of the graph, in grey, a schematic representation of the early-life treatments is provided, with the respective fish symbols representing the presence (+) or absence (-) of adults (F) and predators (P). (From Fischer et al. 2017)

above, in *N. pulcher* subordinate group members may help their dominant breeder pair by participating in territory defence and maintenance as well as by cleaning and fanning eggs and larvae (Taborsky and Limberger 1981). Some subordinates help only a little but appease aggressive breeders by intensive submissive displays (Fischer et al. 2014). These two alternative tactics used to appease dominant breeders are not applied very flexibly. Instead, some individuals specialise in helping and others in showing submissive displays (Kasper et al. 2017, 2018a). The specialisation of subordinate group members in either a submissive or a helper type arises as a consequence of the early environment in which young *N. pulcher* grow up during their first weeks of life. When the two key selective forces of *N. pulcher*, predation risk and social environment, were manipulated in a full-factorial rearing experiment (Fig. 8), they interactively shaped the propensity to show rather more submission or more helping behaviour (Fischer et al. 2017). Interestingly, the propensity to delay dispersal from the natal family unit or to disperse early for independent breeding was also driven by the early experience in predation risk and social environment.

For a social cichlid, the most extreme manipulation of the social rearing environment is to be reared in full social isolation. *Pelvicachromis taeniatus* are socially monogamous cave-breeding cichlid from West Africa. After a period of extensive, biparental brood care, juvenile *P. taeneiatus* live in groups until they reach sexual maturity. When young of this species are reared in complete social isolation, their social behaviours clearly carry the signature of early social deprivation. Compared to

normal, group-reared conspecifics, isolation-reared fish are more aggressive towards conspecifics and, consequently, they are less likely to join a juvenile shoal (Hesse and Thünken 2014). Additionally, these fish are more likely to inspect a predator without a companion (Hesse et al. 2015) and show deficits in sexual behaviour (Hesse et al. 2016).

It remains to be answered why social experience made in the earliest life stage can have such strong and lasting effects on social behaviour. An important factor is the temporal structure of the environment animals live in, which appears to be relatively stable, at least in some cichlids. Developmental plasticity can only be adaptive in environments that are predictable to some degree, that is where current conditions predict future conditions. In such environments cues that young pick up from their social environment may inform them about the intensity and type of competition, they will encounter in the future. This includes cues about local density, sex ratio, or the age and size structure of populations. In addition to this inadvertent information, direct experience from social interactions with siblings, parents, or other group members may significantly contribute to later-life social performance, which may occur by improved opportunities to learn how to behave adequately in different social situations (Taborsky 2016a).

4.3   The (Co-)Evolution of Social Structure and Behaviour

As we have outlined, cichlids show an incredible variation in both social structures and social behaviours, which exists within and among species, populations, and individuals. While this variation might seem daunting, it presents an unparalleled opportunity to explore the degree to which social organisation and social behaviour are linked. Some questions arise naturally—are species (or populations) showing more complex social organisations also behaviourally more complex? Are animals living in larger or socially more diverse groups cognitively more sophisticated? Does stable social structure reflect the existence of stable and defendable resources? Other questions are more nuanced but no less fascinating—can the same neurobiological template produce both social and non-social animals? What effect do the various forms of gene-by-environment interaction (e.g. juvenile experience, social niche availability, food abundance) have on subsequent social behaviour? Is biparental care the basal state required for subsequent evolution of more complex sociality?

For these and a wealth of other questions related to social behaviour, there is very likely a cichlid system well-suited to finding an answer. At the level of sheer numbers, this may not be surprising given almost half of all vertebrates are fish, and one in every 10 species of fish are cichlids. For instance, there are almost 10 times as many species of cichlids as there are primates. Yet cichlids have a number of attributes above sheer species diversity that make them particularly well-suited to studying questions of social behaviour and evolution:

1. Cichlids have some of the best studied, and best resolved phylogenetic relationships of any taxonomic group. Any evolutionary comparison requires a robust scaffolding on which to make comparisons and examine transitions in the traits of interest. With a long history of comparative work that has developed into cutting-edge studies employing genomic and transcriptomic approaches, the opportunity for quantitative comparative work in cichlids is nearly unmatched.

2. Cichlids have a great diversity of social organisations. Within the broad family Cichlidae, the spectrum of sociality ranges from species living as solitary pelagic piscivores to lurking ambush predators mimicking decaying fish, through polyandrous harems of crevice spawners, to cooperative breeders with social organisations approaching the complexity of the most highly social insects, birds, and mammals. This diversity in social structure allows for comparisons at many levels, including life-history and ontogenetic effects, the fitness consequences of living in groups, and the evolutionary trajectories of social systems.

3. A major limitation of many comparative studies is the unavoidable inclusion of confounding variables in the comparative framework. Within cichlids, and especially those in Lake Tanganyika, syntopic populations encounter near identical environments, occurring in mosaic communities and in some cases even living within the same nests (e.g. *L. callipterus* with *T. vittatus* and *L. calliurus*). While there are many communities in which similar species overlap in spatial and temporal distribution, the shell-dwelling communities of Lamprologines are one of the best examples of this shared ecology—abiotic factors are shared, most animals are of similar size, have the same predators and therefore risk regime, and compete over similar physical resources. This overlap in ecology means that many alternative sources of selection on social behaviour can be ruled out, at least within the same populations. Moreover, where variation in ecological factors does exist, for example among nearby populations, this can usefully be used to test hypotheses about the effects of this variation on social behaviour.

4. The rich and varied behavioural repertoire of cichlids provides the raw material for many lines of inquiry concerning the evolution of, and variation in, behaviour. Examining why individuals may behave in different ways under different social or environmental contexts, what the immediate or long-term consequences of these behavioural differences may be, and how relevant sensory information is integrated into behavioural decisions, are all fascinating and timely questions that the rich diversity of cichlid behaviour can help to answer.

5. The ability to work with cichlids in both lab and field, using largely equivalent experimental designs, is a particularly powerful feature of the system. Using cichlids, creating aquarium experiments with realistic social and physical arrangements is relatively straightforward, especially in rock and shell-dwelling species that are typically highly site-specific and defend relatively small areas that can be recreated in captive settings. But the exceptional benefit of cichlids as a study system in behaviour is that these laboratory-based experiments can be directly translated to field settings. For many species, high site-specificity and territoriality mean that researchers are able to return to the same locations and study the same, individually identifiable subjects for extended periods. Thus, the

degree of control and replication typically only found in lab studies can be extended to the field. Obviously, this does not apply for all species, but it pertains for many species including most of the *Lamprologini* of Lake Tanganyika, which remain in the same location for much of their life.

6. Cichlids are typically small and therefore highly amenable to captive breeding and experimentation. Their popularity as aquarium species is testament to this relative ease of care, and their famed parental care behaviour in both mouthbrooding and substrate spawning species leads to high population growth under appropriate conditions. Most species have generation times in the order of 4–6 months, making them suitable for some experimental breeding designs, and the ability to hybridise among species that might vary in a trait of interest also opens up the potential for backcrossing to explore the genetic basis of certain behaviours. In the age of CRISPR-Cas9 gene-editing technologies, the large size and accessibility of fertilised zygotes has already been used to produce genetically-modified lines of *A. burtoni*, and is also being explored in Lamprologines (see below).

5 The Past, Present, and Future of Cichlid Behavioural Research

The study of social behaviour in cichlids has a long history, with reports on the reproductive and social behaviour of jewel cichlids (*Hemichromis bimaculatus*) and the Mozambique Tilapia (*Oreochromis mossambicus*) already well established by the 1950s (Breder 1934; Noble and Curtis 1939; Baerends and Baerends-van Roon 1950). These early studies provide a richly detailed account of a great many aspects of cichlid social interactions, territoriality, courtship, and parental behaviour, which was the origin of modern studies into cichlid behaviour. Since then, cichlid behavioural studies have continued apace, spanning continents and taxonomic groups. These behavioural analyses can be performed in both lab and field, with many studies asking how behaviour changes in different contexts (e.g. Jordan et al. 2016; Groenewoud et al. 2016). Cichlids are also a prime example for advanced cognitive skills in fish (Fernald 2017; Bshary and Brown et al. 2014), including the ability to successfully infer relationships without direct physical contact with individuals (Grosenick et al. 2007; Hotta et al. 2015a, b), the ability to recognise familiar individuals (Kohda et al. 2015) and discriminate them from unfamiliar individuals (dear-enemy effect; Balshine et al. 2017; Weitekamp and Hofmann 2017), and the ability to deceive other conspecifics (Chen and Fernald 2011).

In addition to studies of cognition, cichlids are emerging as a prime system in which to study the structure and function of brain regions associated with social interactions across vertebrate species (O'Connell et al. 2011; Félix and Oliveira 2021). Within the vertebrate brain, two neural circuits are most commonly examined in studies of social behaviour–the Social Behaviour Network (SBN; Goodson 2005;

Newman 1999) and the mesolimbic reward system. The social decision-making network (SDMN) is a higher-order integration of these circuits and is associated with stimulus salience and the regulation of adaptive social behaviours including reproduction, aggression, and parental care. Over the past decades, numerous studies of cichlids, covering a wide array of different aspects including the mechanistic basis of behaviour have been conducted; for example, in *Astatotilapia burtoni* (Greenwood et al. 2008; Maruska and Fernald 2018; O'Connell et al. 2011), *Oreochromis mossambicus* (Almeida et al. 2019), and *N. pulcher* (Kasper et al. 2018a, b; Taborsky et al. 2013). This work is being extended to other cichlid groups, in which representative histological brain atlases are currently being constructed for a number of Lamprologine cichlids (*N. pulcher*: D. Antunes et al., unpublished data; *N. multifasciatus, N. similis, N. brevis, L. ocellatus, L. ornatipinnis, L. meeli, T. temporalis* 'dwarf morph': Lein et al., in preparation). Not only will this vastly expand the number of candidate species, but it will also facilitate studies into patterns of neural activity in response to social stimuli through quantification of immediate early gene (IEG) expression levels (e.g. transcription factors c-Fos, EGR-1) in candidate regions of the SDMN using similar approaches to numerous neuroethological studies involving fishes (Desjardins et al. 2015; Maruska et al. 2013; Roleira et al. 2017; Teles et al. 2015, 2016; Weitekamp and Hofmann 2017). Cichlids are also amenable to CRISPR gene editing and other genetic tools that allow selective manipulation of candidate neural circuits involved in social interactions (Juntti 2019), providing experimental potential to examine candidate mechanistic pathways underlying social behaviour.

In the modern era, cichlid behavioural studies are already taking on a new and exciting aspect with the advent of visual tracking and computational ethology (Rodriguez-Santiago et al. 2020) alleviating many of the difficulties in studying cichlids in the wild or in large social groups. Computer tracking of groups numbering up to thousands of fish is now possible, bringing the analysis of large groups of cichlids under natural conditions within reach (Francisco et al. 2020). In concert with this, approaches such as behavioural decomposition may soon allow an unsupervised machine learning approach to analysing different behavioural states (Fig. 9; Nuehrenberg and Jordan 2019). This technique is already being employed with great success in model organisms such as *Drosophila* and mouse, demonstrating that the behaviour of freely interacting animals can be recorded and analysed using automated processes in incredibly high detail, which can be used also to infer social relationships (Berman et al. 2014). Given the variety of cichlid behaviour, the ease with which these behaviours are expressed under lab conditions, and the strong foundation of cichlid ethology developed over the past 70 years or so, it is easy to foresee that these techniques will translate extremely well to cichlid behavioural research. These approaches have the potential to revolutionise the study of social behaviour in cichlids, and harness the benefits of a rich ethological history combined with cutting-edge technological approaches. Indeed, the future of research on the evolution of social behaviour in cichlids is bright.
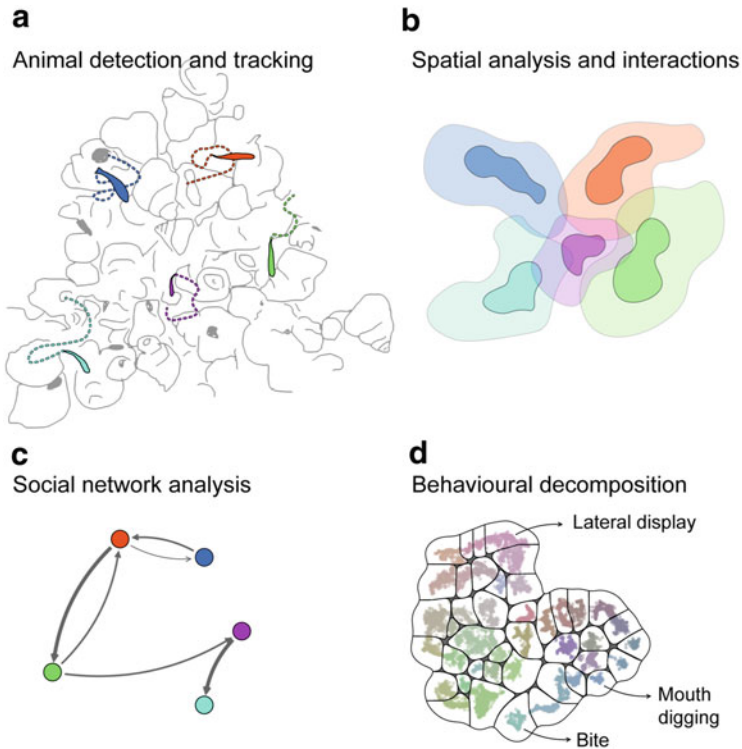
Fig. 9 Future directions for cichlid research will (**a**) utilise the increasing power of automated tracking and machine learning to track cichlid movement, posture, and interactions, (**b**) perform high-resolution spatial analyses, including interactions with environmental structures, (**c**) analyse social networks, and (**d**) use behavioural decomposition techniques, which use kinematic analyses to describe behavioural categories and can be represented in representations like this t-SNE embedding, to complement traditional ethological observations (Figure by Paul Nuehrenberg and Alex Jordan)

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