Studying the evolution of social behaviour in one of Darwin's Dreamponds – a case for the Lamprologine shell-dwelling cichlids

Etienne Lein [1,2], Alex Jordan [1,2]

1. Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz, Germany
2. Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany

* Corresponding author: elein@ab.mpg.de; ajordan@ab.mpg.de

Abstract

The link between the evolution of advanced sociality and cognition has been an important concept across fields and taxonomic boundaries. However, in many study systems, ecological and phylogenetic confounds impair evolutionary inferences drawn when comparing social organization. Here we highlight the value of the shell-dwelling Lamprologine cichlids of Lake Tanganyika in studies of cognitive and social evolution. These species show differences in social organisation, both within and across species, but otherwise exhibit remarkable similarities in their ecology and life-history. We focus on the ecological and social attributes of 15 Lamprologine cichlids that live in permanent association with empty gastropod shells, often in syntopy and with largely overlapping ecological niches. We then discuss difficulties with terminology and categorisation of social organisation, outlining current and emerging methodologies to address these limitations. Our goal is twofold: i) to gather available empirical evidence on the behaviour, life-history, and ecology of shell-dwelling Lamprologine cichlids, highlighting their potential in comparative studies of cognition and evolution, and ii) to stimulate debate and critical appraisal of current terminology and categorisations of social structure, ideally leading to more precise and empirically standardised definitions of sociality in cichlids.

Social interactions are ubiquitous in the animal world, from territorial behaviour in otherwise solitary animals, to brief mating unions, through to permanent social bonds; the consequences of social interactions are complex and far-reaching. When considering the evolution of behaviour, the role of the social environment presents a fascinating and challenging suite of conceptual, theoretical, and empirical problems. At a broad level, the fitness consequences of living socially are well understood (Rubenstein and Abbot 2017; Wilson 2000). Alexander (1974) was the first to note that group-living will only evolve when there are sufficient benefits to offset the costs of increased disease and parasite transmission and intensified competition, and these potential costs have been well studied in a variety of taxa (Booth 1995; Coolen 2002; Krause et al. 2002; Martinez and Marschall 1999; Slotow and Paxinos 1997). The benefits of group living are also well documented (Krause et al. 2002), and generally include increased foraging success (Krebs 1974; Morgan 1988; Pitcher et al. 1982), and reduced per-capita predation risk, encompassing increased predator vigilance (Lima 1995; Lima and Bednekoff 1999; Morgan 1988), predator confusion (Pitcher et al. 1982; Grand and Dill 1999), and predation dilution (Krause et al. 2002; Pitcher 1986). While these general costs and benefits are relatively well understood, understanding the selective pressure exerted by the social environment on individual-level behavioural phenotypes remains difficult. Perhaps the most difficult element of this problem is that social environments are fluid, and the high spatial and temporal variability of exchanges with social partners makes it difficult to understand how these interactions result in selection on behaviour. Moreover, rather than being passive subjects of selection induced by social context, individuals can change the selective environment they experience by moving between social groups, potentially entering contexts that are more favourable in terms of e.g. sex ratio, reproductive opportunities, or decreased competition (Jordan and Brooks 2012; Oh and Badyaev 2010). The fluid nature of social contexts further complicates any analysis of how social context shapes the evolution of behaviour.

Despite the challenges, examinations of the link between the degree of "social complexity" (a metric of how many interactions an individual may experience, and how varied these interactions might be), and an individual's degree of "behavioural complexity" (a range of behaviours an individual can perform), has been a fruitful ground for conceptual development. From early analytical models of the game-theoretic nature of animal behaviour (Grafen and Sibly 1978; Smith 1977), in which the value of any particular strategy should be considered in light of its performance against competing strategies, to empirical tests of the value of different behavioural strategies in varying social regimes (Jordan et al. 2014; Parker 1974), up to broad conceptual syntheses of the value of social context-appropriate responses (Taborsky and Oliveira 2012) – the interaction between social context and individual behaviour has long fascinated researchers. Major questions in the field of social behaviour are still wide open. Why do some species engage more frequently in these social interactions than others? Which factors determine whether an animal lives solitary, in aggregations, or in stable social groups? Although being challenging questions to answer, uncovering the proximate and ultimate factors shaping sociality are essential steps towards an understanding of the evolution of social behaviour. In this paper, we will argue that shell-dwelling cichlids of Lake Tanganyika represent a powerful study system that will yield answers to many of these seemingly insurmountable challenges.

<u>Social evolution and its consequences for behaviour and the mechanisms of behaviour</u>

While living in groups is advantageous for many reasons, there are clearly limitations on the major evolutionary transition to sociality (Szathmáry and Smith 1995). Social behaviour is poorly represented in many taxa, for instance, of the ~48,000 accepted species of spiders (www.wsc.nmbe.ch, 2019), fewer than 100 are considered social by certain standards (Lubin and Bilde 2007). This is likely due to the inherent conflict associated with living in groups of potential competitors (Davies et al. 2012), providing internal threat to these temporally stable "communities of fate". The question then arises as to how individuals manage to navigate such complex social arrangements. The concept of 'social competence' (Taborsky and Oliveira 2012; Varela et al. 2020) has sought to explain the link between the demands of social interactions and the evolution of advanced socially relevant cognitive skills. Social competence is defined as the ability of an animal to adaptively adjust the expression of its social behaviour according to previous social experience and social context, using a number of building blocks including cognitive appraisal, social recognition and memory, and social inference (Oliveira 2013). For example, in *Neolamprologus pulcher*, a Lamprologine cichlid species that forms stable social groups, individuals that had been reared in socially more rich environments show more submissive and less aggressive behaviours in a contest with a more dominant conspecific and thus decrease the probability of being evicted from the territory (Fischer et al. 2015; Nyman et al. 2017).

Associated with this increased cognitive complexity is the development of mechanisms that produce social behaviour. In addition to the various genetic, endocrinological, and other physiological processes underlying social behaviour, it is neuroanatomy, and patterns of neural activity, that have received most research attention. While the general concept has been formulated before in many variations, the best known is the *Social Brain Hypothesis* (SBH; Dunbar 1998; Humphrey 1976; Whiten and Byrne 1988). This hypothesis argues that sociality poses increased cognitive challenges that lead to the evolution of individuals with more complex cognitive and neuroanatomical traits (Jolly 1966; Whiten and Byrne 1988). When first published, the hypothesis aimed to test the idea that primates living in larger social groups showed disproportionately large brains (usually indexed as neocortex volume) relative to their body size (Dunbar 1992; Dunbar 1998; Whiten and Byrne 1988). Arguing that evolution typically constitutes an economical process that balances costs and benefits, the high operating expenses and surplus of brain tissue (beyond the body's pure physical requirements) were suggested to be compensated for by enhanced cognitive skills. These increased cognitive skills in turn allowed individuals to cope with the challenges related to a complex social life-style and accrue benefits of group living; this hypothesis therefore proposed a direct evolutionary relationship between sociality, cognition, and brain size. In the following years, the SBH was expanded to attain a wider evolutionary application by extending the concept also to other group-living, non-primate taxa, such as ungulates, carnivores, bats, birds, and even insects – however with varying and inconclusive results (Dunbar and Shultz 2007; Lihoreau et al. 2012).

<u>Disentangling complexity in social and ecological dimensions</u>

In order to investigate the putative link between sociality and cognitive capacity, it is essential to eliminate equally plausible alternative theories that have been brought forward as explanations for observed variations in brain size or cognitive capacity more generally (Dunbar and Shultz 2007). In the case of primates, brain size has been associated for instance with the way in which food is processed ("extractive foraging hypothesis"; Gibson 1986; Parker and Gibson 1977), with dietary preferences (higher unpredictability of fruits as compared to leaves; Clutton-Brock and Harvey 1980; DeCasien et al. 2017), or with differences in home ranges (larger ranges potentially require more sophisticated mental maps; Clutton-Brock and Harvey 1980). At the same time the SBH has been criticised for inaccuracy related to the (initial) concept of "social complexity" (Dunbar and Shultz 2007; Healy and Rowe 2007; Logan et al. 2018).

In a formal analysis of the evolution of behaviour, cognition, and neuroanatomy it is necessary to separate social from other ecological factors (Barton 1996; Dunbar and Shultz 2017; Reader and Laland 2002; Shumway 2010). In a previous study investigating seven species of the cichlid fish tribe Ectodini, habitat complexity and measures of social organization were found to co-vary, confounding a resolution of the sources of selection driving changes in brain size (Pollen et al. 2007). In order to address these issues, a common strategy is to explicitly incorporate all recorded ecological variables into a single statistical analysis (DeCasien et al. 2017; Shultz and Dunbar 2006). An example for this approach is the use of multiple regression analysis. However, in studies with small sample sizes and strong multicollinearity between variables, this kind of statistical analysis can regularly prevent a clear separation, and thus interpretation, of predictors (Deaner et al. 2000; Gonzalez-Voyer et al. 2009). However, even with the most robust statistical tools the interaction amongst social and other ecological factors remains a conceptual problem in understanding the sources of selection acting on sociality. By contrast, a study system exhibiting minimal variation with respect to all relevant ecological variables, but high variation in the variable of interest – in this case social complexity – would be ideal for testing predictions made by the SBH (Gingins and Bshary 2016), namely that increased social complexity drives the evolution of cognitive capacity. Here we make the argument that the shell-dwelling Lamprologine cichlids of Lake Tanganyika offer just such a system for understanding the co-evolution of social structure, behaviour, cognition, and neuroanatomy.

<u>Cichlid fish as model systems</u>

Compared to taxa such as primates (e.g. DeCasien et al. 2017; Reader and Laland 2002) or birds (e.g. Beauchamp and Fernández-Juricic 2004; Kabadayi et al. 2016; Shultz and Dunbar 2010), fish have traditionally played a comparatively minor role in the study of cognitive evolution (Bshary et al. 2014). Nevertheless, the utility of fishes as a model system has been recognised by a handful of fairly recent multi-species comparisons (Chojnacka et al. 2015; Gingins and Bshary 2016; Pollen et al. 2007; Reddon et al. 2017; Soares et al. 2015), or studies investigating intraspecific variation in the social environment (Arnold and Taborsky 2010; Fischer et al. 2015; Kotrschal et al. 2012; Taborsky et al. 2012; Triki et al. 2019; Wismer et al. 2014). Given their impressive diversity in terms of social organization and the exploitation of different ecological niches (Fryer and Iles 1972; Meyer 1993), it is not surprising that Tanganyikan cichlids

have been the focus in the majority of these studies. In a study of seven species of the Tanganyika cichlid tribe Ectodini, social and physical environment were associated with the volume of major brain regions. Specifically, telencephalic size was found to be larger in monogamous as compared to polygamous species; at the same time however, habitat complexity (measured as rugosity) showed a similar trend (Pollen et al. 2007). A comparative study including 39 Tanganyikan cichlid species from six different tribes found diet type (whose rank was based on increasing prey motility) to be negatively correlated with brain weight (Gonzalez-Voyer et al. 2009), a result that was interpreted to be linked to the more complex social structure associated with diet via habitat (although habitat complexity itself was not directly correlated with brain size; Gonzalez-Voyer et al. 2009).

A subsequent study by the same authors investigated 43 Tanganyikan cichlid species and found mating competition (which correlates with mating system type; Gonzalez-Voyer et al. 2008) to be correlated negatively with telencephalon volume, whereas habitat complexity (measured as rugosity) was found to be positively correlated with telencephalon volume (Gonzalez-Voyer and Kolm 2010), thus confirming previous results (Pollen et al. 2007). By contrast, the study found no association between diet type and telencephalon size (Gonzalez-Voyer and Kolm 2010) as had been predicted by the authors beforehand on the basis of prior results (Gonzalez-Voyer et al. 2009). This exemplifies well the complex effects and interactions that different environmental variables such as habitat (e.g. rugosity, depth) or diet (e.g. feeding type) on the one hand (Huber et al. 1997; Sylvester et al. 2010), and social variables (e.g. mating system type, parental care) on the other hand (Gonzalez-Voyer and Kolm 2010; Gonzalez-Voyer et al. 2009; Pollen et al. 2007; Shumway 2008), exert on brain size evolution in Tanganyikan cichlids (and analogously on other vertebrate study systems, like carnivores or primates; Gittleman 1986; Dunbar and Shultz 2017).

The interpretation of the results in these and similar studies is made difficult when study animals are sourced from commercial collectors. Sourcing animals from exporters risks creating confusion over collection location, ontogeny and rearing conditions of "wild-caught" animals (which may have spent some generations in collector's and exporter's ponds outside the lake itself; AJ *personal obs.*), and even confusion over the species assignment itself, given that closely related species may have overlapping distributions separated only by local differences in habitat. As an example of this latter point, *T. temporalis* and *T.temporalis* 'dwarf morph' occur in close proximity but occupy different ecological niches and have divergent life-histories (Takahashi an Ota 2016, Takahashi 2004). Despite clear variation in social behaviour and organization, both these variants are described as *T. temporalis* in the aquarium trade and in much scientific literature. If an understanding of ecological factors mediating evolution of a trait is sought, it is necessary to have an accurate estimate of those ecological factors, especially considering that short-distance changes in conditions can create large differences in the selective environment experienced by an individual (Bolnick et al. 2007; Maciejewski et al. 2020; Richardson et al. 2014). Local environmental conditions vary substantially in Lake Tanganyika, and such small-scale variation has been shown to affect selection regimes in other aquatic environments (Maciejewski et al. 2020). Because of the lack of detail on

actually experienced selective environments, it is challenging to draw conclusions about the interaction among ecological conditions and the evolutionary process when assuming species-level attributes.

Instead of approaches that seek to explicitly account for a number of confounding variables, an alternative strategy is to identify a set of species in which these confounds are minimized (Shumway 2008). We argue the Lamprologine shell-dwelling cichlids of Lake Tanganyika are one of the best examples of such a system. The shell-dwelling cichlids are a species group that possess many valuable attributes in studies of social evolution and behaviour: (i) at 15-23 species, a powerful comparative sample (Table 1), (ii) with close and well-resolved phylogenetic relationships, (iii) similar sizes; similar ecological factors, including (iv) overlapping dietary niches with similar feeding modalities, and (v) sympatric patterns of distribution, or even syntopic mosaic communities with similar risk environments on the macro-habitat level, and (vi) a low variation in environmental complexity, due to their resembling, permanent, association with empty snail shells; (as a result of this shell-dwelling lifestyle, it is conceivable that other life-history traits, including brood size or age at sexual maturity, are similar across these cichlid species). Crucially, despite these remarkable similarities, the shell-dwelling Lamprologine cichlids are highly divergent with regard to their social structure. It is this combination of attributes that makes shell-dwelling cichlids so well-suited for investigations into the influence of the social environment on cognitive and behavioural evolution. In the following section we explain in detail each of these attributes across the shell-dwelling cichlid species.

<u>Attributes of Lake Tanganyikan shell-dwelling cichlids</u>
One of the Great Lakes in the East African Rift Valley, Lake Tanganyika is shared between the countries of Tanzania, Zambia, D.R. Congo and Burundi. The world's second largest body of freshwater and home to a multitude of endemic species, Lake Tanganyika is famed for its astonishing diversity of cichlid fishes (currently 208 valid species; estimates reach up to 241 species; Ronco et al. 2019), which, all but a few exceptions, inhabit its nearshore benthic zone (Konings 2015).

Phylogeny
A model system for ecology and evolution (Salzburger et al. 2005) and textbook example in evolutionary biology for rapid and extensive adaptive radiation (Kocher 2004; Seehausen 2006; Takahashi and Koblmüller 2011), Lake Tanganyikan cichlids have been subject to intense scientific interest spanning a period of over 120 years (R.T. Günther described the first cichlid species in 1894, G.A. Boulenger in 1897). Among other important achievements, this sustained research has recently yielded one of the best resolved molecular phylogenies for any radiation to date (Ronco et al., *accepted*). This detailed knowledge of the phylogenetic relationships of Tanganyikan cichlids generally, and Lamprologine (Sturmbauer et al. 2010) or shell-dwelling cichlids (Koblmüller et al. 2007) specifically, enables a powerful use of the comparative method and is a fundamental prerequisite for testing evolutionary hypotheses (MacLean et al. 2012). The fact that Tanganyikan cichlids evolved more rapidly as compared to other vertebrate lineages potentially makes it easier to identify salient selection pressures (Pollen et al. 2007). Especially in closely-related species, whose variability is expected to be limited by similar developmental constraints, discovering such

variability for a trait across closely related species might be evidence that this trait has been shaped by selection pressure (Pollen et al. 2007).

While the species flock of Tanganyikan cichlids comprises sixteen different tribes, it has been the monophyletic tribe of Lamprologine cichlids that, as a consequence of their immense diversity in social organization and sophistication of social behaviours (Kornfield and Smith 2000), has received arguably the most attention by ethologists. Notably, the overwhelming majority of all recognized and suspected cases of cooperative breeding in fish (76-84%) can be found within this tribe (Heg and Bachar 2006; Taborsky 1994), which comprises 87 valid lacustrine species to date (Ronco et al. 2019), making Lamprologine cichlids a model system for the integrative study of social behaviour (Jordan et al. 2020).

Shell use as a unifying trait
Unique to the substrate-breeding tribe of Lamprologini, a number of species have specialized in the use of empty snail shells (Koblmüller et al. 2007; Sato and Gashagaza 1997; Fig. 1). Due to Lake Tanganyika's alkaline waters (De Wever et al. 2005) that prevent their rapid dissolution, the calcareous shells of molluscs of the genus *Neothauma* accumulate in extensive layers on the lake benthos (Cohen and Thouin 1987), where they are used by a number of cichlid species as brooding chambers and/or as shelters from predators or conspecifics (Table 1). While Lamprologine cichlids are morphologically the most diverse tribe of Tanganyikan cichlids (Clabaut et al. 2007), most cichlids permanently dwelling in shells, confined by the snail shell's morphology, exhibit close resemblance in body size (Table 1), which is regarded as a direct adaptation to this specific life style (Büscher 1998; Gashagaza et al. 1995; Kohler 1998; Sato and Gashagaza 1997; Takahashi and Ota 2016).

Diet
Earlier studies that have analysed stomach contents in a selection of shell-dwelling cichlid species suggest that many species in question predominantly prey on small benthic invertebrates and zooplankton (Table 2). The conclusion that these food items constitute an important dietary staple for these small-sized cichlids is corroborated by earlier work which suggests that Lamprologines are carnivorous (Gashagaza and Nagoshi 1986; Hori 1983). Further support derives from behavioural observations in the natural habitat, which indicate that a majority of shell-dwelling cichlids (including the species previously examined for stomach contents) exhibit functionally and kinematically similar foraging behaviour, involving either picking small prey from the substrate and/or snatching them directly from the water column (Table 2). The case of *Lamprologus* sp. 'ornatipinnis zambia', a species with both sex-specific and large seasonal shifts in the consumed diet (Fryer and Iles 1972; Gordon and Bills 1999), demonstrates the caution that must be taken when interpreting results on small sample sizes and those of unknown specific collection conditions. Like all members of the family Cichlidae however, Tanganyika cichlids possess pharyngeal jaws which exhibit strong phenotypic plasticity, and pharyngeal jaw morphology is known to strongly correlate with dietary preferences (Takahashi and Koblmüller 2011), making morphometrical analyses a helpful piece of information when drawing conclusions with respect to individual, population, and species level dietary

niche. However, as of now, data on pharyngeal jaw morphology are relatively sparse, and inferences based on stable isotopes are a similarly effective proxy for assessing dietary niches. Stable isotope analyses conducted on fifteen different shell-dwelling cichlid species demonstrate broadly similar trophic niches (F. Ronco, W. Salzburger, *in preparation*), although there are notable differences for some species (e.g. *N. similis* having considerably lower $\delta^{15}N$ than *L.* sp. 'ornatipinnis zambia'). Since brain size and overall head shape are phenotypically integrated in Tanganyikan cichlids, and head shape is correlated with feeding mode (Tsuboi et al. 2014), a system exhibiting only little variation in feeding ecology is of importance when studying brain evolution. Overall, current data confirm the general assertion that shell-dwelling cichlids share the same trophic level, relatively similar dietary preferences, and functionally closely related foraging modes.

Distribution

Most shell-dwelling cichlids are found syntopically (i.e. occupying the same macrohabitat, occurring together in the same locality, and being observable in close spatial proximity; Rivas 1964) with some others occurring at least sympatrically (see Table 1 for specific details; Koblmüller et al. 2007; Sato and Gashagaza 1997). Shell-dwelling cichlids occupy physical environments ranging from muddy or sandy substrates interspersed with few gastropod shells (e.g. *Lamprologus ocellatus*), to rubble-covered substrate with small localized clusters of shells (e.g. *Neolamprologus brevis*), up to so-called "shell beds" which are extensive areas composed entirely of empty shells (e.g. *Neolamprologus multifasciatus*; Sato & Gashagaza 1997). These differences in microhabitat structure could represent a source of variation in habitat complexity (Gutiérrez et al. 2003) with potential effects in the social domain (Shumway 2010; Shumway et al. 2007). Indeed, shell beds and localized clusters of shells appear to harbour high densities of individuals as well as a relatively high species diversity per unit of area (Sato and Gashagaza 1997), and thus represent a potential confounding effect, yet as we detail below, this can be partially alleviated (§ "Outstanding challenges in the study of social and cognitive evolution").

Predation

Species of similar size living syntopically, like the shell-dwelling cichlids, likely face a similar set of heterospecific predators in their environment (Fryer and Iles 1972). This suite of predators may fluctuate with regard to abundances and proportions, resulting from density-related effects on the micro-habitat level with consequences for predator encounter rates (Wrona and Dixon 1991). Different populations of the Lamprologine cichlid *N. pulcher*, for instance, have been reported to face different predation pressures, which in turn are reflected in changes in social group structure (Groenewoud et al. 2016). While this source of variation implies a potential confounding factor (van der Bijl and Kolm 2016) – particularly when comparing across non-sympatric species – a logical remedy is to focus investigations specifically to those shell-dwelling species that occur within overlapping, mosaic communities (for an example cf. Sato and Gashagaza 1997). Alternatively, or in addition to this, different populations of the same species at different localities allow the quantification of the effect of these sources of variation and an explicit examination of their significance for cognitive divergence among populations.

<u>Diverse and highly-developed social and cognitive capacities</u>

Sophisticated social behaviours

Cichlid social behaviour – involving courtship displays and pair-bond reinforcement, numerous different submissive, affiliative and aggressive behaviours exhibited during contests – encompasses an immense range of behaviours, contexts and communicatory channels (Jordan et al. 2020). It was the wealth of behaviours observed in captive cichlids that caught the attention of early ethologists (Aronson 1949; Baerends and Baerends-van Roon 1950; El-Zarka 1956; Noble 1937; Noble and Curtis 1939; Wickler 1962), who created ethograms rivalling those of mammals in their behavioural sophistication and diversity. Current ethograms of Lamprologines, such as those for the cooperatively breeding cichlid *N. pulcher* and the shell-dwelling cichlid *N. multifasciatus* contain between 13-18, respectively 12, distinct visually observable social behaviours (Sopinka et al. 2009; Taves et al. 2009; Kohler 1998; Lein et al. *in prep.*), affording an inspection of the social relationships that individuals within these species share at a fine-grained level.

Cognitive capacity

Despite their reputation as relatively primitive vertebrates, a number of fish species including species from the tribes of Lamprologini and closely-related Haplochromini have been demonstrated to possess a range of sophisticated cognitive skills. These involve the ability to (individually) recognize conspecifics (*N. pulcher*: Balshine-Earn and Lotem 1998; Frostman and Sherman 2004; Hert 1985; Kohda et al. 2015; Saeki et al. 2018; *Julidochromis transcriptus*: Hotta et al. 2017; *A. burtoni*: (Weitekamp and Hofmann 2017), to memorize socially relevant information for multiple days (*J. transcriptus*: Hotta et al. 2014) and to use experience as a way to modulate social behaviour during contests (*A. burtoni*: Alcazar et al. 2014; *N. pulcher*: Fischer et al. 2015). Furthermore, it has been shown that members of these cichlid tribes possess the ability to create mental representations of hierarchies (*J. transcriptus*: Hotta et al. 2015a; Hotta et al. 2015b; *A. burtoni*: Grosenick et al. 2007), the ability to tactically deceive conspecifics (*A. burtoni*: Desjardins et al. 2012) or redirect aggression to a third party as a form of conflict management (*Julidochromis regani*: Ito et al. 2018). While it still remains to be tested to which extent the shell-dwelling cichlids match their close relatives in this striking level of cognitive capacity, numerous teleost fish have evolved a suite of adaptations to acquire, process, store and act on information (definition by Shettleworth 2009), cognitive abilities comparable to those of birds and mammals (Brown et al. 2011; Bshary et al. 2002; for a review on fish social cognition see Bshary et al. 2014). Cichlids therefore appear particularly well-suited to investigations into the co-evolution of sociality and cognition (Bshary and Brown 2014; Bshary et al. 2002).

Neuroanatomy and an evolutionary conserved "social brain"

Brain regions considered relevant for social behaviour are conserved across the five major vertebrate lineages, including mammals and teleost fish (O'Connell and Hofmann 2011; O'Connell and Hofmann 2012). Of crucial importance in this context are two neural circuits, the Social Behaviour Network (SBN; Goodson 2005; Newman 1999) and the mesolimbic reward system. Together these circuits integrate into the higher order social decision-making network (SDMN) where stimulus salience is evaluated, and where

adaptive social behaviours including reproduction, aggression, and parental care are regulated (O'Connell and Hofmann 2012). Although the proposed homology relationships for most of SDMN-associated nuclei do not necessarily imply conserved function (Goodson and Kingsbury 2013), the SDMN regions are logical targets for investigating mechanisms of cognitive evolution in response to social pressures in cichlids. To that end, as a first step representative histological brain atlases are currently being constructed on the basis of referential information (Burmeister et al. 2009; Munchrath and Hofmann 2010; Simões et al. 2012) for a number of Lamprologine cichlids (*N. pulcher*: D. Antunes et al., unpublished data; *N. multifasciatus, Neolamprologus similis, N. brevis, L. ocellatus, L.* sp. 'ornatipinnis zambia'*, Lepidiolamprologus meeli, Telmatochromis temporalis* 'dwarf morph': Lein et al., *in preparation*). These morphological atlases describe SDMN-associated nuclei within the brain and enable the comparison of volumes and neuronal densities of brain (sub-)structures and SDMN nuclei. In birds, neuronal density in the telencephalon has been shown to be a better predictor for cognitive performance as compared to brain size (Olkowicz et al. 2016). Consequently, quantifications on the cellular level in candidate areas of the brain (i.e. SDMN-associated nuclei) constitute an important step towards refinement beyond comparably coarse measurements of cognitive capacity, like (relative) brain size (e.g. Gonzalez-Voyer et al. 2009; Huber et al. 1997; Tsuboi et al. 2015; van Staaden et al. 1994) or volumes of larger brain areas such as the telencephalon or hypothalamus (e.g. in Gonzalez-Voyer and Kolm 2010; Pollen et al. 2007; Shumway 2008). Indeed, the use of coarse neuroanatomy as an explanatory variable in understanding the function or evolution of the nervous system has come under criticism (Chittka et al. 2012; Healy and Rowe 2007; Pollen and Hofmann 2008).

Over the past decades a handful of African cichlid species have emerged as model systems in the field of neuroethology, with numerous studies covering a wide array of different aspects including the mechanistic basis of behaviour (*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; Kasper et al. 2018b; Taborsky et al. 2013). Leaning on this extensive body of knowledge, morphological brain atlases in shell-dwelling cichlids will 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. Such transcriptional profiling is a frequently used method in neuroethological studies involving fishes (Desjardins et al. 2015; Maruska et al. 2013; Roleira et al. 2017; Teles et al. 2015; Teles et al. 2016; Weitekamp and Hofmann 2017), and appears to increasingly corroborate the functional significance of SDMN-nuclei in encoding social behaviour.

Further advantages
Field-based studies
A major strength of the Lamprologine system is that natural experiments in Lake Tanganyika are tractable, due to the small size of study animals, their small home ranges, and their site fidelity. Moreover, although access to Lake Tanganyika remains somewhat difficult, conditions at the Lake are highly conducive for underwater field work. Lake Tanganyika is one of the clearest body of freshwater in the world (Konings 2015) and downwelling surface irradiance reaches the lake benthos in near-shore waters (Langenberg et

al. 2002). This means that shell-dwelling cichlids, which typically inhabit depths of ~10m, can be observed with relative ease in their natural habitat through SCUBA-diving (Konings 2015). Home ranges of the shell-dwelling cichlids species are often very small (e.g. *N. multifasciatus* or *T. temporalis* 'dwarf morph': approx. 30 cm; Schradin and Lamprecht 2002; EL *personal obs.*) and individuals usually restrict their movements to around and between those shells that lie within their own territory boundaries (e.g. Jordan et al. 2016; Konings 2015; EL, *personal obs.*). This is of high practical utility, since it allows researchers to monitor the location and behaviour of multiple individuals simultaneously and continuously using either direct observation or by placing camera arrays. The latter method is particularly advantageous considering that, after prior installation of multi-camera arrays, individual fish can be observed in a minimally invasive way, and both their natural behaviour and the community species composition can be captured as accurately as possible (Widmer et al. 2019). Moreover, a strong site fidelity and the association of individuals with their "home shells", whose position can be manipulated, can make it possible to manipulate distances among individuals in a group, modify available resources (Jordan et al. 2016), or even manipulate the shells themselves (Bose et al. 2020). These manipulations facilitate investigations into the potential of social plasticity in different species of shell-dwelling cichlids, allow examinations of the effect of early-life social environment on the acquisition of social competence (Fischer et al. 2015; Fischer et al. 2017b; Nyman et al. 2017) or assessments with respect to brain development (Fischer et al. 2015).

Laboratory-based studies
Small body sizes, short generation times (Koblmüller et al. 2008), the possibility to obtain large numbers of offspring under semi-natural laboratory settings, in combination with their unproblematic conservation status (*Least concern* in all cases, https://www.iucnredlist.org/), also allow for the establishment of sizable populations in laboratory conditions and therefore make shell-dwelling cichlids amenable for investigating e.g. neuroanatomy or cognitive performance with a high sampling throughput. By contrast, in other commonly investigated study systems like primates ethical or logistical considerations and resulting limited sample sizes often hamper the interpretability of the obtained data. A promising future avenue for studying social behaviour lies furthermore in the use of CRISPR gene editing and other genetic tools that allow to selectively manipulate candidate neural circuits involved in social interactions (Juntti 2019), or the use of immersive virtual reality (VR) to experimentally control and alter an individual's perception of its social environment. The adaptation of these techniques in fish has been pioneered in zebrafish (Hruscha et al. 2013; Liu et al. 2018; Stowers et al. 2017) and has recently also been applied to cichlids (Alward et al. 2020; Juntti et al. 2016). Thus, an extension to non-traditional model systems like shell-dwelling cichlids seems not only realizable, but crucially, would also yield highly interesting new insights given their evolutionary divergence into distinct social strategies (Juntti 2019).

Outstanding challenges in the study of social and cognitive evolution
To properly test the link between social and environmental conditions, cognitive and brain evolution it is essential to identify those factors of social living that affect the cognitive workload of an animal (Bergman and Beehner 2015). As we have described above, one limitation comes where often large variation in

ecology and geography among species being compared obscures any effects of differences in social systems. However, a second and perhaps more difficult problem comes where the classification of social complexity is inadequate, weakening subsequent comparisons to quantitative traits like brain morphology. Initial proxies for social complexity like *average group size* (Dunbar and Shultz 2007) have proven inadequate (e.g. Sandel et al. 2016), and more recent definitions have, for instance, emphasized the importance of differentiated relationships in stable social groups (Bergman and Beehner 2015; Shultz and Dunbar 2006), arguing that the necessary behavioural flexibility is cognitively challenging and therefore exerts a selective pressure driving cognitive evolution. Although this definitional refinement has gained traction in certain areas of social evolution research (e.g. in primatology: Fischer et al. 2017a; Kappeler 2019; Lukas and Clutton-Brock 2018; Ramos-Fernandez et al. 2018), likely due to constraints in the ability to resolve social structure in sufficient detail many studies still rely on categorical or coarse quantitative classifications (e.g. Ashton et al. 2018; DeCasien et al. 2017; Fox et al. 2017; Kverková et al. 2018; Weisbecker et al. 2015). Similarly, in cichlid research, categorical classifications of sociality (based for instance on qualitative descriptions of mating system or parental care type; often from hobbyist publications) are still rather the norm than the exception. Cooperative breeding species like *N. pulcher* or the shell-dweller *N. multifasciatus* are regularly attributed to be *highly social*, *highly advanced social*, or interchangeably, (*highly*) *socially complex* (e.g. Fischer et al. 2017b; Taborsky and Wong 2017; Jordan et al. 2016; Pisanski et al. 2015; Mileva et al. 2009). The justification for this label varies, but has been connected, amongst others, to the existence of social stratification, individualized relationships, cooperation, and/or frequent social interactions (Fischer et al. 2017b; Pisanski et al. 2015; Reddon et al. 2016). While there is no doubt that *N. pulcher* experiences a complex social environment, it remains unclear which combination of social factors generates the complexity experienced by an individual, and how these factors combine and scale. This knowledge is essential for cross-species comparisons in which the robustness of the data and the conclusions that can be drawn from them strongly hinges on a fine resolution in the independent variable of interest.

As pointed out before elsewhere (e.g. Bergman and Beehner 2015), qualitative classifications are inherently problematic when applied to questions dealing with social and cognitive co-evolution, since their bearing on the cognitive load can generate ambiguous and contradictory predictions. For instance, it has been argued that monogamy is highly complex, since bond maintenance is thought to require an increased level of social acuity, deception (Schillaci 2006) and/or coordination abilities (Emery et al. 2007; Shultz and Dunbar 2007). On the other hand, the management of multiple relationships and more complex interactions in polygamous systems has been connected with high cognitive demands alike (e.g. Sawaguchi 1992). As for cooperative breeding, a recent study on sixteen nominally cooperatively and independently breeding Lamprologine species detected no positive correlation between cooperative breeding and increased brain size (Reddon et al. 2016), which might support the argument that it is not cooperative breeding *per se* that is cognitively challenging (Thornton and McAuliffe 2015).

A major limitation of any such species level approaches is that a single species can often occur in monogamous or polygamous associations, depending on population, resource availability, location within a community, or time of year (see Table 2; Desjardins et al. 2008; Heg and Bachar 2006; Limberger 1983; Smuts et al. 2008), making an either/or classification inherently problematic. Mating system-based classifications of social complexity are further complicated because often no clear distinction between social (i.e. inferred through behavioural observations) and genetic (i.e. based on parentage analysis) mating systems is being made (Sefc 2011). This ambiguity, potentially resulting from definitional obscurities in combination with a general uncertainty concerning mating systems in Lamprologine cichlids (Taborsky et al. 2019), has recently sparked a controversy within the community (Dey et al. 2019; Tanaka et al. 2018), emphasising the difficulties in using a mating system-based approach to the definition of social complexity. An alternative, but equally problematic categorical division in Lamprologine cichlids is often made between *grouping* and *non-grouping* species, which may then be further broken down as *(highly) social* and *less social* (e.g. Balshine et al. 2017; Hick et al. 2014). Although the required criterion of a link between sociality and cognitive load appears more straightforward in this scheme, *grouping* and *non-grouping* at best offers a similar proxy for social complexity as does *group size*, insofar as it describes a coarse number of (theoretical) interaction partners. Classifications such as *grouping* vs. *non-grouping* are further weakened by the difficulty in assigning animal group membership based on anthropocentric metrics of e.g. distance. Although it is straightforward to define individuals as belonging to the same group if they are within some distance range of one another, this may not reflect the perceived sensory environment of the animals being studied (Jordan and Ryan 2015). The term "social" implies the occurrence of interactions between conspecific individuals, which can occur over large visual ranges (and in other modalities) than are easily captured by casual observations of physical proximity. As an example, the typical distances over which harems of *N. multifasciatus* interact is much smaller than the equivalent distance in *L. ocellatus* harems (Gordon and Bills 1999; Jordan et al. 2016; Schradin and Lamprecht 2002; Trillmich et al. 1999), and therefore it cannot be concluded that *N. multifasciatus is* grouping while *L. ocellatus is not*. Even if rigorously defined, these dichotomous classes leave no room for intermediate levels of organisation, into which many species realistically naturally fall (Krause et al. 2002). *N. pulcher*, for instance, exhibits strong variation with regard to group sizes; although groups typically consist of 7-9 individuals on average, groups with only three and up to 38 individuals have been observed in the natural habitat (Balshine et al. 2001; Taborsky et al. 2005). Likewise, for *N. multifasciatus*, and *T. temporalis* 'dwarf morph', reports of group sizes range from 2-20 individuals (Konings 2015, Schradin & Lamprecht 2002; Kohler 1998; Bose et al., *in preparation*) and 2-7 individuals (Takahashi et al. 2012), respectively.

A quantitative alternative is the representation of conspecific individuals in the form of social networks (Jordan et al. 2016; Wey et al. 2008). In social networks, each individual is represented as a node that can share a connection (= "edge") with another node based on a defined criterion, such as the presence of a behavioural, spatial, or temporal association between the two nodes (Croft et al. 2008). Social network theory (SNT) has previously been applied to different contexts in the study of Lamprologine cichlids (e.g. in the context of intra-group social dynamics: Hellmann and Hamilton 2019; in the context of extended

phenotypes: Jordan et al. 2016; in the context of investigating dominance interactions and spatial associations: Dey et al. 2013; in the context of general reciprocity: van Doorn and Taborsky 2012; in the context of behavioural types: Schuerch et al. 2010). Despite these various cases of application, however, the utility of SNT for conceptualizing Lamprologine social complexity has not been realised. As an alternative to mating system- or proximity-influenced classifications a social network-based approach that seeks to approximate social complexity on the basis of interaction data in an objective, quantitative manner would allow to capture the social complexity in its multidimensional nature, arising as the simultaneous interplay of several contributing factors (e.g. the number of different interaction partners, the frequencies with which they interact, and the qualities of these interactions). In contrast to the term *grouping*, which may suffer from confounding effects of proximity, group cut-offs in social networks ("network boundaries") can be defined explicitly based on recorded interaction data (Laumann et al. 1989). On the other hand, and in contrast to a classifications based on dichotomous categories, variations in group size and their suggested implication for social complexity (Groenewoud et al. 2016) are well quantified in a social network approach, in which any number of individuals (or even heterospecifics, which have been suggested to contribute to social complexity; Bshary et al. 2014) can theoretically be aggregated into the analytical unit.

Most crucially and contrary to broad or binary classifications schemes, a quantitative approach achieved through social network analysis (SNA) would afford a better resolution of the independent variable (i.e. social complexity) and therefore allow for a stronger test of the hypothesized positive relationship between social complexity and cognitive capacity. A previous study investigating different populations of *N. pulcher* found a considerable inter-population variability in the size (i.e. number of individuals) and composition of social groups, resulting from local differences in predator abundance (Groenewoud et al. 2016). Not least because many shell-dwelling cichlids share sympatric patterns of distribution with *N. pulcher* (Konings 2015), it is conceivable that analogous effects of variation in the risk environment also affect intraspecific variation in social complexity in shell-dwelling cichlids. Intraspecific variation in the social environment has recently been shown to affect the size of brain parts involved in socially relevant cognitive functions in the bluestreak cleaner wrasse *Labroides dimidiatus* (Triki et al. 2019). While such changes represent an insurmountable obstacle for binary classification schemes, variation on this scale can be addressed by means of SNA and thereby create additional refinement in the social dimension.

Emerging quantitative approaches to address current limitations

A reasonable criticism of social network approaches is that essential detail on behavioural interactions is lost in the compression of data to network edges. This problem can arise for two reasons. The first is that human observation skills are restricted to attending to one or two focal individuals at a given time (although see Pruitt and Pinter-Wollman (2015) for a study in which the personality and behaviour of 40 individuals were, allegedly, simultaneously recorded by a single observer). This restriction on human attention necessarily means that social networks must be constructed via successive focal sampling of individuals (e.g. Jordan et al. 2016), thereby reducing the amount of data collected per individual, especially under the time constraints induced by SCUBA based field work. The second is that many different behaviours that

are observed may be simplified to edges representing broader categories such as "aggressive interactions". This may be required because certain behaviours are rare and so creating networks on each behaviour results in overly sparse networks that cannot easily be analysed, and this problem is exacerbated when sampling times are short. As such, the potential for SNA to improve resolution of social structure and behaviour may be constrained by the ability to collect sufficient data. To date this criticism has been justified, but modern approaches in behavioural ecology are well-poised to overcome these constraints.

Recently, the explosion of computer vision and machine learning algorithms have made it possible to automatically track both the location and the posture of animals under controlled conditions (Brown and De Bivort 2018), and these techniques have even been extended to complex underwater environments including Lake Tanganyika (Francisco et al. 2020). With these technologies, which are based on training artificial neural networks to detect fish in natural scenes, it is increasingly feasible to record and subsequently automatically analyse the behaviour of anywhere from one to hundreds of animals in incredible detail. These high-throughput methodologies will revolutionise the field of behavioural ecology, and are particularly applicable to Lacustrine underwater contexts. While it is easiest to work in clear water with animals that are easily distinguishable from their background, these approaches have already been proven effective under challenging environmental settings such as those posed by an aquatic environment like Lake Tanganyika, where conditions of low light, murky water, crypsis of the focal animal (e.g. in *T. temporalis* 'dwarf morph', Takahashi 2019), occurrences of plankton blooms (Plisnier et al. 1999; Salonen et al. 1999), heterogeneous backgrounds, or backdrops with varying light incidence, occur at times. These automated tracking approaches can rapidly generate rich datasets on the identity, position, motion, and posture of all group members under observation, relying on consumer grade cameras (Francisco et al. 2020). As such, rich behavioural and association networks can be populated and analysed without the constraints imposed by human observation, even in the natural contexts in which individuals within a species or a population have evolved.

A second great opportunity presented by automated tracking is the ability to analyse behavioural states in great detail. In addition to the objective, quantitative metrics of social complexity achievable by tracking numerous individuals in real time, computational methods allow to objectively quantify and understand the behaviours themselves. These techniques, known broadly as "behavioural decomposition", have become generally available and are enjoying increasing popularity, allowing us to transition from qualitative ethological description to quantitative analyses of behaviour (Berman et al 2014). These approaches take time series data of animal postures and subdivide these into discrete clusters, either with supervised or unsupervised approaches. Behavioural decomposition employs clustering with stochastical neighbour embedding and subsequently separates clusters into distinct states that can be interpreted as stereotypical behaviours (Berman et al. 2014; Klibaite et al. 2016). Alternatively, machine learning algorithms can be trained on a small, annotated subset of the recorded time series to detect the annotated behaviours, massively increasing the quantity of behavioural data able to be gathered (Kabra et al. 2013). With these approaches the scoring of behavioural traits becomes consistently repeatable across studies and species,

while also reducing the potential for human subjectivity influencing data, which may lead to disagreement over categories or definitions of behaviour (Brown and De Bivort 2018). These approaches also have the potential to identify previously unrecognized behaviour, thus adding further resolution to behavioural analyses. Lamprologine cichlids are particularly well-suited to these approaches, given their high site fidelity, small home ranges, and small elevation from the benthos, all of which allow relatively straightforward video recording and subsequent tracking. Together with the emerging field of animal linguistics that investigates syntax patterns and semantics in social behaviour, these approaches will allow to capture the true richness of interactions between these fascinating animals. Finally, the ability to produce aquarium hybrids, and to potentially observe such hybrids in the wild (Koblmüller et al. 2007) make it conceivable to establish and study "intermediate" social phenotypes in this study system, which would eventually allow for an even more nuanced analysis of social complexity.

Conclusion

We argue that Tanganyikan shell-dwelling cichlids represent a unique system for assessing the effect of the social environment on brain/cognitive evolution. Currently used classifications of sociality or social complexity, however, fall short of capturing a relevant metric of the cognitive demands related to the social environment of individuals within differing groups, populations, or species. As an alternative, and in line with recent developments towards more meaningful appraisal of social complexity within the field of comparative cognition, we therefore propose a shift towards a social network-based approach in combination with emerging tracking technologies that strives to incorporate the multi-dimensional nature of social complexity in an information theoretical framework. In this way, we can bring cichlids to the forefront of research into the social mechanisms leading to brain and behavioural evolution.

Investigating the proposed link between social and cognitive evolution is contingent upon a holistic understanding of the respective studied system. Using Tanganyikan shell-dwelling cichlids in such a framework will consequently require filling still existing gaps and uncertainties with regard to the ecology of a few, currently understudied, species. These data will be particularly pertinent for questions surrounding the real extent of ecological diversity amongst shell-dwelling species. With more information on hand shell-dwelling cichlids have then the potential to provide a truly unique model system to address the predictions made by the social brain hypothesis and related conceptual frameworks.

Table 1. Syntopies, body lengths and modality of shell use in permanently shell-dwelling cichlids; coloured cells denote further potential candidate species for shell-dwelling, albeit with currently sparse information; SL: standard length, TL: total length.

Species	Confirmed syntopy [species]	Length [cm SL | TL]	Shell use		References
			brooding	shelter	
Neolamprologus multifasciatus BOULENGER 1906	- *L. sp. 'ornatipinnis zambia'* [a,d] - *L. ocellatus* [d] - *L. meeli* [a,g,h] - *N. calliurus* [a,h] - *N. brevis* [c,h] - *T. temporalis 'dwarf morph'* [a,h?] - *T. vittatus* [a,h] - *A. sp. 'compressiceps shell'* [a,g] - *L. callipterus* [a,h] - *N. caudopunctatus* [i]	1.90 – 2.45 cm SL (median) [d] 2.5 – 4 cm TL [e]	✓ [1, a-f]	++ [1, a-f]	Lein et al., in prep.[a]; Büscher 1992b [b]; Jordan et al. 2016 [c]; Kohler 1998 [d]; Rossiter 1993 [e]; Schradin and Lamprecht 2002 [f]; Bills 1996 [g]; Sato and Gashagaza 1997 [h]; pers. comm. H. Büscher [i]
Neolamprologus similis BÜSCHER 1992	- *L. speciosus* [2, a,b] - *L. callipterus* [d] - *N. caudopunctatus* [d]	2.66 – 3.58 cm SL (range of sizes from n=6 ind.) [a]	✓ [3, c]	++ [3, c]	Büscher 1992b [a]; Büscher 1998 [b]; Konings 2015 [c]; pers. comm. H. Büscher [d]
Neolamprologus brevis [4] BOULENGER 1899	- *N. calliurus* [a,c,d,e,f] - *L. sp. 'ornatipinnis zambia'* [b?,f,i] - *L. ocellatus* [a,b,f,i] - *L. meeli* [f] - *L. callipterus* [f] - *T. temporalis 'dwarf morph'* [a,f?] - *T. dhonti 'shell'* [f] - *T. vittatus* [f] - *N. multifasciatus* [b,g,f] - *N. mondabu 'dwarf morph'* [f]	3.9 – 4.4 cm SL (range of averages from Kombe and Gitaza populations) [b] 3.55 – 4.55 cm SL (Wonzye pop.) [5, e]	✓ [a,b,c,f,h]	+++ [a-e]	Lein et al., in prep. [a]; Bills 1996 [b]; Konings 1998 [c]; Konings 2015 [d]; Ota et al. 2012 [e]; Sato and Gashagaza 1997 [f]; Jordan et al. 2016 [g]; Büscher 1991 [h]; Büscher 1998 [i]; pers. comm. H. Büscher [j]; pers. comm. A. Konings [k]

Species	Confirmed syntopy [species]	Length [cm SL | TL]	Shell use		References
			brooding	shelter	
Neolamprologus brevis [4] BOULENGER 1899	- *L. speciosus* [h] - *L. meleagris* [h] - *L. laparogramma*[i,k] - *L. boulengeri* [j] - *L. signatus* [k]				
Neolamprologus calliurus [4] BOULENGER 1906	- *N. brevis* [a,c,d,e] - *N. multifasciatus* [a] - *T. temporalis 'dwarf morph'* [a] - *L. callipterus* [a,c,d,e] - *T. vittatus* [a,c,d,e]	3.52 – 6.04 cm SL (Wonzye pop.) [5, d]	✓ [c,e]	+ [6, a,d]	Lein et al., in prep. [a]; Bills 1996 [b]; Konings 2015 [c]; Ota et al. 2012 [d]; Sato and Gashagaza 1997 [e]
Neolamprologus mondabu 'dwarf morph' BOULENGER 1906	- *L. ocellatus* [b] - *L. callipterus 'shell'* [a] - *N. brevis* [b] - *T. dhonti 'shell'* [b] - *A. sp. 'compressiceps shell'* [a] (- *T. temporalis 'dwarf morph'* [b?])	3.28 – 4.82 cm SL (range of sizes from n=8 ind.) [a]	✓ [7, a,b]	++ [7, a]	Gashagaza et al. 1995 [a]; Sato and Gashagaza 1997 [b]
Lamprologus sp. 'ornatipinnis zambia' [8] POLL 1949	- *N. multifasciatus* [a,d] - *L. ocellatus* [b-d] - *L. meeli* [a,b,d] - *L. laparogramma* [b,f] - *N. brevis* [b?,c,d] - *A. sp. 'compressiceps shell'* [a,b] - *L. callipterus* [d] - *T. vittatus* [d]	3.8 – 4.3 cm SL (range of averages from Kombe, Mbita Island, Musende Rocks and Gitaza populations) [b]	✓ [a-d]	++ [a,b]	Lein et al., in prep. [a]; Bills 1996 [b]; Büscher 1998 [c]; Sato and Gashagaza 1997 [d]; pers. comm. H. Büscher [e]; pers. comm. A. Konings [f]

Species	Confirmed syntopy [species]	Length [cm SL | TL]	Shell use		References
			brooding	shelter	
	- *T. temporalis 'dwarf morph'* [a,d?] - *L. signatus* [e,f]				
Lamprologus ocellatus STEINDACHER 1909	- *N. brevis* [a,b,d,f] - *N. mondabu 'dwarf morph'* [d] - *L. meeli* [a,b,d,e] - *L. sp. 'ornatipinnis zambia'* [a,b,d,f] - *T. dhonti* [d] - *L. callipterus* [a,b,d] - *N. multifasciatus* [c,d] - *L. laparogramma* [b] - *T. vittatus* [d] - *L. signatus* [h] - *L. boulengeri* [h] - *T. temporalis 'dwarf morph'* [d?, g]	3.6 – 3.9 cm SL (range of averages from Mbita Isl. and Musende Rocks populations) [b]	✓ [a,b,d,e,g]	++ [9, a,b,e,g]	Lein et al., in prep. [a]; Bills 1996 [b]; Kohler 1998 [c]; Sato and Gashagaza 1997 [d]; Trillmich et al. 1999 [e]; Büscher 1998 [f] Konings 1998 [g]; pers. comm. H. Büscher [h]
Lamprologus speciosus BÜSCHER 1991	- *L. meleagris* [a,b] - *N. brevis* [a,b]	2.78 – 3.61 cm SL [a]	✓ [10, a-c]	++ [11, a,b]	Büscher 1991 [a]; Büscher 1998 [b]; Konings 2015 [c]
Lamprologus meleagris [12] BÜSCHER 1991	- *L. speciosus* [a,b] - *N. brevis* [a,b]	2.83 – 4.28 cm SL (range of sizes from n=7 ind.) [a]	✓ [a-c]	++ [11, a,b]	Büscher 1991 [a]; Büscher 1998 [b]; Konings 2015 [c]
Lamprologus callipterus BOULENGER 1906	- *N. calliurus* [a,b,d] - *T. vittatus* [a,b,d] - *T. temporalis 'dwarf morph'* [a,d?] - *L. ocellatus* [a,b,d]	3.15 – 11.6 cm SL [c,e]	✓ [b-d]	+ [13, b,c]	Lein et al., in prep. [a]; Bills 1996 [b]; Sato 1994 [c]; Sato and Gashagaza 1997 [d]; Schütz and

Species	Confirmed syntopy [species]	Length [cm SL | TL]	Shell use		References
			brooding	shelter	
Lamprologus callipterus BOULENGER 1906 (continued)	- *L. sp. 'ornatipinnis zambia'* [a,d] - *N. multifasciatus* [a,d] - *L. meeli* [a,d] - *N. brevis* [d] - *A. sp. 'compressiceps shell'* [a,b] - *N. similis* [f] - *N. caudopunctatus* [f]				Taborsky 2000 [e]; pers. comm. H. Büscher [f]
Lepidiolamprologus meeli [14] POLL 1948	- *L. ocellatus* [a-c] - *T. temporalis 'dwarf morph'* [a,c?, e] - *N. brevis* [b,c] - *L. sp. 'ornatipinnis zambia'* [a-c] - *N. multifasciatus* [a,c] - *T. vittatus* [c] - *L. callipterus* [c] - *A. sp. 'compressiceps shell'* [a,b] - *N. pulcher 'shell'* [e] - *L. boulengeri* [e]	4.31 – 4.95 cm SL (range of averages from Kombe, Mbita Isl. and Musende Rocks populations) [b] 5.74 – 7.24 cm TL (Wonzye pop.) [d]	✓ [b-d]	++ [a,b,d]	Lein et al., in prep. [a]; Bills 1996 [b]; Sato and Gashagaza 1997 [c]; Sunobe and Munehara 2003 [d]; pers. comm. H. Büscher [e]
Telmatochromis temporalis 'dwarf morph' [15] BOULENGER 1898	- *N. multifasciatus* [a,b?] - *L. meeli* [a,b?] - *A. sp. 'compressiceps shell'* [a,b?] - *L. ocellatus* [b?, g] - *L. sp. 'ornatipinnis zambia'* [a,b?] - *N. brevis* [a,b?] - *N. mondabu 'dwarf morph'* [b?] - *L. callipterus* [a,b?] - *T. vittatus* [b?, g]	2.08 – 3.82 cm SL (range of averages from Chibwensolo, Mbita Isl. and Wonyze populations) [c,e] 2.1 – 3.1 cm SL (Wonzye pop.)	✓ [a,b,d,e]	++ [a,d,e,f]	Lein et al., in prep. [a]; Sato and Gashagaza 1997 [b]; Takahashi 2004 [c]; Takahashi 2019 [d]; Takahashi et al. 2012 [e]; Takahashi et al. 2009 [f]; pers. comm. H. Büscher [g]

Species	Confirmed syntopy [species]	Length [cm SL | TL]	Shell use		References
			brooding	shelter	
	- *T. dhonti* [b?] - *N. pulcher* 'shell' [g]				
Telmatochromis vittatus BOULENGER 1898	- *L. callipterus* [a-e] - *L. meeli* [e] - *N. calliurus* [a-e] - *N. multifasciatus* [a,e] - *T. temporalis* 'dwarf morph' [a,e?,f] - *A. sp.* 'compressiceps shell' [a,b]	< 4.5 cm TL female [c] 2.62 cm SL ('sneaker') [c] 4.57 cm SL ('satellite') [c] 5.5 cm SL ('territorial') [c] 6.41 cm SL ('pirate') [c]	✓ [16, c-e]	++ [17, c]	Lein et al., in prep. [a]; Bills 1996 [b]; Ota and Kohda 2006a [c]; Ota and Kohda 2006b [d]; Sato and Gashagaza 1997 [e]; pers. comm. H. Büscher [f]
Altolamprologus sp. 'compressiceps shell' [18] BOULENGER 1898	- *N. multifasciatus* [a] - *T. temporalis* 'dwarf morph' [a,e?] - *T. dhonti* 'shell' [e] - *L. sp.* 'ornatipinnis zambia' [a] - *L. callipterus* [a] - *L. callipterus* 'shell' [c,e] - *T. vittatus* [a,b] - *L. meeli* [a,b] - *L. ocellatus* [e] - *N. brevis* [e] - *N. mondabu* 'dwarf morph' [c,e]	3.69 – 5.7 cm SL (range of sizes from n=11 ind.) [c]	✓ [c-e]	++ [a,c,d]	Lein et al., unpub. data [a]; Bills 1996 [b]; Gashagaza et al. 1995 [c]; Konings 2015 [d]; Sato and Gashagaza 1997 [e]
Lamprologus callipterus 'shell morph' [19] BOULENGER 1906	- *A. sp.* 'compressiceps shell' [a,b] - *N. brevis* [b] - *L. ocellatus* [b] - *T. dhonti* 'shell' [b]	4.3 – 5.11 cm SL (range of sizes from n=10 ind.) [a]	✓ [a,b]	+++ [a]	Gashagaza et al. 1995 [a]; Sato and Gashagaza 1997 [b]

Species	Confirmed syntopy [species]	Length [cm SL | TL]	Shell use		References
			brooding	shelter	
	- *N. mondabu 'dwarf morph'* [a,b] (- *T. temporalis 'dwarf morph'* [b?])				
Neolamprologus sp. "Mwila" - undescribed species -	- *L. meeli* [a] - *L. callipterus* [a] - *T. dhonti* [a] - *N. brevis?* [a]	5 – 7 cm TL [a]	✔ [a]	- [a]	Karlsson & Karlsson 2020 [a]
Lamprologus laparogramma BILLS & RIBBINK 1997	- *L. ocellatus* [a] - *L. sp. 'ornatipinnis zambia'* [a,d] - *L. meeli* [a] - *N. brevis* [c,d]	2.78 – 3.56 cm SL [a] approx. 3 – 5 cm TL [b]	✔ [20, a]	+ [20, a]	Bills 1996 [a]; Konings 2015 [b]; pers. comm. H. Büscher [c], pers. comm. A. Konings [d]
Lamprologus signatus POLL 1952	- *L. sp. 'ornatipinnis zambia'* [c,d] - *L. ocellatus* [c] - *N. brevis* [d]	2.74 – 3.57 cm SL [a] approx. 3 – 5 cm TL [b]	✔ [20, a]	+ [20, a]	Bills 1996 [a]; Konings 2015 [b]; pers. comm. H. Büscher [c], pers. comm. A. Konings [d]
Neolamprologus pulcher 'shell' [21] TREWAVAS & POLL 1952	- *T. vittatus* [a] - *L. meeli* [b] - *T. temporalis 'dwarf morph'* [b]	approx. <7.5 cm TL [a]	? [22]	++ [22, a]	Lein et al., unpub. data [a]; pers. comm. H. Büscher [b]
Telmatochromis dhonti 'shell' BOULENGER 1919	- *L. callipterus 'shell'* [a] - *N. mondabu 'dwarf morph'* [a] - *A. sp. 'compressiceps shell'* [a] - *N. brevis* [a]	?	✔ [a]	?	Sato & Gashagaza 1997 [a]

Species	Confirmed syntopy [species]	Length [cm SL | TL]	Shell use		References
			brooding	shelter	
	- *L. ocellatus* [a] (- *T. temporalis* 'dwarf morph' [a?])				
Lepidiolamprologus boulengeri [23] STEINDACHER 1909	- *L. ocellatus* [b] - *L meeli* [b] - *N. brevis* [b]	5 – 7 cm TL [a]	✓ [a]	+ [24, a]	Konings 2015 [a]; pers. comm. H. Büscher [b]
Neolamprologus caudopunctatus POLL 1978	- *L. callipterus* [a] - *T. vittatus* [a] - *N. multifasciatus* [d] - *N. similis* [d]	4.45 – 5.05 cm SL [a] (Mbita pop.) 6.5 – 7.5 cm TL [b] 4.5 – 6 cm TL [c] (Kasakalawe pop.)	✓ [b]	?	Ochi and Yanagisawa 1999 [a]; Schädelin et al. 2012 [b]; Schädelin et al. 2015 [c]; pers. comm. H. Büscher [d]
Neolamprologus wauthioni [25] POLL 1949	?	?	?	?	Konings 2015

1. (With)in some populations of *N. multifasciatus* (e.g. Mbete Bay, Cape Kapembwa) individuals are also known to brood and hide in cracks or in-between stones (Kohler 1998, pers. comm. H. Büscher).

2. Not explicitly stated; based on combined information on geographical and depth distribution (Büscher 1992b, Büscher 1998).

3. Some populations of *N. similis* (Mbete Bay, Cape Kapembwa; Kohler 1998) are known to brood and hide in cracks or in-between stones (Büscher 1992b).

4. *N. brevis* and *N. calliurus* are usually treated as two separate species (Sturmbauer et al. 1994, Koblmüller et al. 2007, Konings 2015, Ronco et al. 2019), but Ota et al. (2012) see in what has been described as *N. brevis* the sub-adult stage of *N. calliurus* (and refer to both as N. brevis). These two species are referred to as *N. brevis* ("out of the nest [of *L. callipterus*]"), respectively as *N. brevis* ("in the nest [of *L. callipterus*]"), in Sato and Gashagaza (1997).

5. In their analysis of body sizes Ota et al. (2012) refer to these as individuals from shell beds/separated shells on sand bottom and individuals in shell patches/in midwater aggregations, which we interpret to refer to members of the species *N. brevis* and *N. calliurus*, respectively.

6. Due to the large size of males shells are used as shelter mainly by females (Ota et al. 2012).

7. *N. mondabu* females dig a hole at the side of *Neothauma* shells and spawn their eggs on the shells' outer surface; the hole also serves as shelter. Territorial males use shells as shelters (Gashagaza et al. 1995).

8. According to Konings (2015).

9. When no shells are immediately accessible, to escape predators this species might instead dive into the sandy bottom (Konings 2015).

10. Not stated explicitly.

11. When no shells are immediately accessible, to escape predators this species might instead dive into the sandy bottom (Konings 2015, pers. comm. H. Büscher) or flee (Büscher 1991).

12. It is suspected that *L. meleagris* and *L. stappersi* are indeed the same species (Konings 2015). Since for *L. stappersi* PELLEGRIN 1927 only the holotype exists in museum collections, comparisons to other taxa are difficult (Ronco et al. 2019).

13. Due to the large size of territorial males, shells are exclusively used by females and certain types of males with alternative reproductive strategies (Sato 1994).

14. Also called *Neolamprologus meeli / Lamprologus meeli*.

15. It has been demonstrated that *T. temporalis* 'dwarf morph' is a genetically distinct dwarf-sized ecomorph of the rock-dwelling *T. temporalis* (Takahashi 2004; Takahashi et al. 2009; Winkelmann et al. 2014). At the time Sato & Gashagaza published their work on shell-brooding cichlids (1997), the status of this species was still under investigation. It is therefore unclear whether the authors had observed subadult rock-dwelling individuals, or alternatively, adult dwarf-size individuals at the study locations (denoted with a superscript "?" in the "Confirmed syntopy [species]" column).

16. Spawning might also occur in small crevices (Ota & Khoda 2006a).

17. Only small individuals hide in shells (Ota & Khoda 2006a).

18. Listed as currently potentially undescribed species in Ronco et al. (2019).

19. The attribute 'shell morph' was chosen here to distinguish this population, that had been originally described by Gashagaza et al. (1995) and in which also territorial males are small enough to enter empty *Neothauma* shells, from the standard *L. callipterus*.

20. *L. laparogramma* and *L. signatus* typically live in holes which are dug into the muddy substrate, but when shells are abundant in muddy habitats they also make use of them as shelters and breeding sites (Bills 1996).

21. Known to occur at Mwina, Mutondwe Island, Zambia (Lein et al., unpub. Data; pers. comm. H. Büscher). Usually N. pulcher broods and seeks shelter between and underneath flat and small round stones that are maintained through digging (Balshine et al. 2001; Taborsky et al. 2005).

22. The *N. pulcher* Mwina population constructs their nests from stone bricks as well as from empty *Neothauma* shells (Lein et al., unpub. data). Observations in the Lake, however, suggest that the fish only occasionally access these shells and instead mainly use the interstitial space (pers. comm. H. Büscher).

23. Also called *Neolamprologus boulengeri*

24. Females of this species use shells only sometimes as shelters, whereas males flee over the sand when threatened (Konings 2015).

25. Originally described as *Lamprologus wauthioni.*

Table 2. Mating systems and diets of permanently shell-dwelling cichlids; coloured cells denote further potential shell-dwelling species, albeit with currently sparse information.

Species	Mating system	Diet			References
		gut content	*jaw morphology*	*feeding behaviour*	
Neolamprologus multifasciatus BOULENGER 1906	polygyny/polyandry/ polygynandry [a,b,e]	mainly copepods, microfilamentous and unicellular algae, other small invertebrates [b]	relatively large canines in upper and lower jaw [1, b]	snatching by-drifting (zoo-) plankton [b,c,d,f] (copepods); picking benthic invertebrates [c,f]	Bose, submitted. [a]; Kohler 1998 [b]; Konings 2015 [c]; Rossiter 1993 [d]; Schradin and Lamprecht 2002 [e]; Lein et al., in prep. [f]
Neolamprologus similis BÜSCHER 1992	polygyny, polyandry or polygynandry [a]	copepods, crustaceans, insect larvae, diatoms, algae [b]	?	snatching zooplankton (copepods) [c]; picking benthic invertebrates [c]	pers. comm. H. Büscher to Heg and Bachar 2006 [a]; Büscher 1992b [b]; Konings 2015 [c];
Neolamprologus brevis [2] BOULENGER 1899	monogamy - bigamy [3, a,e,f]	copepods [b,d,g]	?	snatching by-drifting plankton [a-c]; feeding on invertebrates [a]	Konings 2015 [a]; Bills 1996 [b]; Ota et al. 2012 [c]; Poll 1956 [d]; Sato and Gashagaza 1997 [e], Büscher 1991 [f]
Neolamprologus calliurus [2] BOULENGER 1906	polygyny/ polygynandry [3, a-c]	?	?	snatching of by-drifting zooplankton [a,b]; feeding on invertebrates [a]	Konings 2015 [a]; Ota et al. 2012 [b]; Sato and Gashagaza 1997 [c]

Species	Mating system	Diet			References
		gut content	*jaw morphology*	*feeding behaviour*	
Neolamprologus mondabu 'dwarf morph' BOULENGER 1906	polygyny [a]	Chironomidae? copepods? [4, b]	?	picking prey from the substrate surface or sediment [4, b]	Gashagaza et al. 1995 [a]; Yuma 1994 [b]
Lamprologus sp. 'ornatipinnis zambia' [5] POLL 1949	monogamy [a,b,e] - bigamy [e] - polygyny [a,b,d]	Chironomidae, copepods, ostracods [c]	jaw: enlarged canines [c] pharyngeal jaw: suggests benthic arthropod feeder [c]	picking invertebrate prey from substrate surface or sediment [a,b]	Lein et al., in prep. [a]; Bills 1996 [b]; Gordon and Bills 1999 [c]; Konings 2015 [d]; Sato and Gashagaza 1997 [e]
Lamprologus ocellatus STEINDACHER 1909	monogamy [a,b,c,e] - polygyny [a-f]	Chironomidae, ostracods [c]	?	picking invertebrate prey from substrate surface or sediment [a,b,d]; snatching of by-drifting zooplankton [d]	Lein et al., in prep. [a]; Bills 1996 [b]; Brandtmann 2002 [c]; Konings 2015 [d]; Sato and Gashagaza 1997 [e]; Trillmich et al. 1999 [f]
Lamprologus speciosus BÜSCHER 1991	polygyny [a]	mainly insect larvae (Chironimidae); copepods [b]	?	picking invertebrate prey (insect larvae, small shrimps) from substrate surface; snatching by-drifting plankton [a]	Konings 2015 [a]; Büscher 1991 [b]

Species	Mating system	Diet			References
		gut content	*jaw morphology*	*feeding behaviour*	
Lamprologus meleagris [6] BÜSCHER 1991	polygyny [a]	mainly insect larvae (Chironimidae); copepods [b]	?	picking invertebrate prey (insect larvae, small shrimps) from substrate surface; snatching by-drifting plankton [a]	Konings 2015 [a]; Büscher 1991 [b]
Lamprologus callipterus BOULENGER 1906	polygyny [a,b]	shrimp, copepods [b,c]	?	picking shrimp from the substrate surface or sediment [c]; feeding on shrimp and fry [c]	Mitchell et al. 2014 [a]; Sato 1994 [b]; Yuma 1994 [c]
Lepidiolamprologus meeli [7]	monogamy- [a-c] polygyny [8, 9, b,c]	?	?	picking invertebrate prey from substrate surface or sediment [a]; feeds from hovering position over the substrate [a,b]; occasionally preying on small shell-dwellers [a]	Bills 1996 [a]; Konings [b]; Sunobe and Munehara 2003 [c]
Telmatochromis temporalis 'dwarf morph' [10] BOULENGER 1898	polygyny [a]	?	six anteriormost teeth on premaxillae	feeding of epilithic algae [a]	Takahashi et al. 2012 [a]; Takahashi 2004 [b]

Species	Mating system	Diet			References
		gut content	*jaw morphology*	*feeding behaviour*	
			enlarged; small lateral teeth [b]		
Telmatochromis vittatus BOULENGER 1898	polygyny? [a]	?	?	feeding on filamentous algae and/or zooplankton [b]; eggs of heterospecifics [c]	Ota and Kohda 2006b [a]; pers. comm. M. Hori to Ota and Kohda 2006a [b]; Bruintjes & Taborsky 2011 [c]
Altolamprologus sp. 'compressiceps shell' [11] BOULENGER 1898	polygyny? [12, a]	shrimp? [12, b]	?	picking shrimp from the substrate surface [12, b]	Konings 2015 [a]; Yuma 1994 [b]
Lamprologus callipterus 'shell morph' [13] BOULENGER 1906	polygyny [a]	shrimp? copepods? [14, b,c]	?	picking shrimp from the substrate surface or sediment [14, c]	Gashagaza et al. 1995 [a]; Sato 1994 [b]; Yuma 1994 [c]
Neolamprologus sp. "Mwila" - undescribed –	?	?	?	?	Karlsson & Karlsson 2020
Lamprologus laparogramma BILLS & RIBBINK 1997	monogamy [a,b]	?	large canines [b]	picking of zooplankton and small invertebrates [b,c]	Bills and Ribbink 1997 [a]; Bills 1996 [b]; Konings 2015 [c]

Species	Mating system	Diet			References
		gut content	*jaw morphology*	*feeding behaviour*	
Lamprologus signatus POLL 1952	monogamy [a,b]	?	large canines [b]	picking of zoo-plankton and small in-vertebrates [c]; feeding from a resting position on the substrate [b]	Bills and Ribbink 1997 [a]; Bills 1996 [b]; Konings 2015 [c]
Neolamprologus pulcher 'shell' [15] TREWAVAS & POLL 1952	monogamy [a,d,e] - polygyny [16, a,d,e]	copepods? [16, c]	?	snatching of by-drifting zooplankton [f]	Desjardins et al. 2008 [a]; Gashagaza 1988 [b]; Gashagaza and Nagoshi 1985b [c]; Limberger 1983 [d]; Taborsky and Limberger 1981 [e]; pers. comm. H. Büscher [f]
Telmatochromis dhonti BOULENGER 1919	monogamy [a] - polygyny [a]	invertebrates? midge larvae? [17, b]	?	?	Sato & Gashagaza 1997 [a]; Konings 2015 [b]
Lepidiolamprologus boulengeri [18] STEINDACHER 1909	monogamy-polygyny [a]	?	?	?	Konings 2015 [a]

Species	Mating system	Diet			References
		gut content	*jaw morphology*	*feeding behaviour*	
Neolamprologus caudopunctatus POLL 1978	monogamy [a,b]	ostracods, insect larvae, copepods, algae [d]	?	picking invertebrates from the substrate surface and water column [c]	Schädelin et al. 2012 [a]; Schädelin et al. 2015 [b]; Konings 2015 [c]; Büscher 1992a [d]
Neolamprologus wauthioni [19] POLL 1949	?	?	?	?	Konings 2015

1. Kohler (1998) suspects that these large canines are possibly connected with intra- and inter-specific conflict.

2. *N. brevis* and *N. calliurus* are usually treated as two separate species (Sturmbauer et al. 1994, Koblmüller et al. 2007, Konings 2015, Ronco et al. 2019), but Ota et al. (2012) see in what has been described as *N. brevis* the sub-adult stage of *N. calliurus* (and refer to both as *N. brevis*). These two species are referred to as *N. brevis* ("out of the nest"), respectively as *N. brevis* ("in the nest"), in Sato and Gashagaza (1997).

3. Sato & Gashagaza (1997) describe the mating system as mono-bigamous for those individuals that are found outside the nest of *L. callipterus*, and polygamous for those individuals that are found inside the nest, which we interpret to refer to members of the species *N. brevis* and *N. calliurus*, respectively.

4. Information based on different (non-shell-dwelling) population.

5. According to Konings (2015).

6. It is suspected that *L. meleagris* and *L. stappersi* are indeed the same species (Konings 2015). Since for *L. stappersi* PELLEGRIN 1927 only the holotype exists in museum collections, comparisons to other taxa are difficult (Ronco et al. 2019).

7. Also called *Neolamprologus meeli / Lamprologus meeli*

8. Sunobe & Munehara (2003) refer to this species as *Neolamprologus meeli*.

9. Bills (1996) refers to this species as *Neolamprologus hecqui*.

10. It has been demonstrated that *T. temporalis* 'dwarf morph' is a genetically distinct dwarf-sized ecomorph of the rock-dwelling *T. temporalis* (Takahashi 2004; Takahashi et al. 2009; Winkelmann et al. 2014).

11. Listed as currently potentially undescribed species in Ronco et al. (2019).

12. Information based on different (non-shell-dwelling) population.

13. The attribute 'shell morph' was chosen here to distinguish this population, that had been originally described by Gashagaza et al. (1995) and in which also territorial males are small enough to enter empty *Neothauma* shells, from the standard *L. callipterus*.

14. Information based on different (non-shell-dwelling) population.

15. Also known as *N. brichardi*; This population is known to occur at Mwina, Mutondwe Island, Zambia (Lein et al., unpub. data). Usually N. pulcher broods and seeks shelter between and underneath flat and small round stones that are maintained through digging (Balshine et al. 2001; Taborsky et al. 2005).
16. Information based on different (non-shell-dwelling) populations.
17. Information based on different (non-shell-dwelling) populations.
18. Also called *Neolamprologus boulengeri*
19. Originally described as *Lamprologus wauthioni.*

Contribution Statement

Etienne Lein and Alex Jordan conceptualized the article. Etienne Lein performed the literature search and together with Alex Jordan drafted and revised the manuscript critically. Both authors approved the manuscript in its final version for submission.

Data Accessibility

All associated data are available at DRYAD (doi: to be uploaded upon publication).

Conflict of Interest

The authors declare no conflict of interest

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