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Social motivation and conflict resolution tactics as potential building blocks of sociality in cichlid fishes

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ABSTRACT

Even closely related and ecologically similar cichlid species of Lake Tanganyika exhibit an impressive diversity of social systems, and therefore these fishes offer an excellent opportunity to examine the evolution of social behaviour. Sophisticated social relationships are thought to have evolved via a building block design where more fundamental social behaviours and cognitive processes have been combined, incrementally modified, and elaborated over time. Here, we studied two of these putative social building blocks in two closely related species of cichlids: *Neolamprologus pulcher*, a group-living species, and *Telmatochromis temporalis*, a non-grouping species. Otherwise well matched in ecology, this pair of species provide an excellent comparison point to understand how behavioural processes may have been modified in relation to the evolution of sociality. Using social assays in both the laboratory and in the field, we explored each species' motivation to interact with conspecifics, and each species' conflict resolution tactics. We found that individuals of the group living species, *N. pulcher*, displayed higher social motivation and were more likely to produce submission displays than were individuals of the non-grouping species, *T. temporalis*. We argue that the motivation to interact with conspecifics is a necessary prerequisite for the emergence of group living, and that the use of submission reduces the costs of conflict and facilitates the maintenance of close social proximity. These results suggest that social motivation and conflict resolution tactics are associated with social complexity, and that these behavioural traits may be functionally significant in the evolution and maintenance of sociality.

Contents

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1. Introduction

Sociality is not a single cohesive unit of behaviour, but instead is comprised of a diverse set of socially relevant actions and cognitive processes (Goodson, 2013). Complex social behaviours are thought to have evolved from a combination of basic behavioral units. Examples include the tendency to approach conspecifics, recognition and discrimination of individuals, and the use of tactics to resolve conflicts at minimal cost (Soares et al., 2010). Small behavioural changes, mediated by subtle alterations in the underlying physiological machinery, are gradually added and modified to form complex social phenotypes (Goodson et al., 2005; Donaldson and Young, 2008; Soares et al., 2010; O'Connell and Hofmann, 2011; Zayed and Robinson, 2012). Therefore, in order to understand the emergence of complex social behaviour and group living lifestyles, it is necessary to understand how these basic behavioural building blocks have changed in form and function during the divergence of social systems.

The explosive radiation of the African cichlid fishes has generated an impressive diversity of species with considerable variation in morphology, ecology, and behaviour and has made this family a classic ecological, evolutionary, and behavioural model system (Meyer et al., 1994; Barlow, 2002; Kocher, 2004). The lamprologine cichlid tribe of Lake Tanganyika, East Africa, shows particularly remarkable diversity in social behaviour among its more than 80 species (Kuwamura, 1986; Konings, 1998; Day et al., 2007; Sturmbauer et al., 2010). As a result, this group offers excellent opportunities for comparative social behaviour research. Of special note, the lamprologine cichlids count amongst their ranks all known cooperatively breeding fishes (Taborsky and Limberger, 1981; Taborsky, 1994; Heg and Bachar, 2006). These cooperative species live in relatively permanent social groups in which non-breeding subordinates assist the dominant breeding pair in their reproductive efforts. A high level of social complexity characterizes cooperative breeding societies, with group members that interact frequently, and have individualized relationships (Freeberg et al., 2012; Dey et al., 2013). Cooperative breeding has emerged multiple times among the lamprologine cichlids, and is derived from the pair breeding system typical for cichlids (Dey et al., in review), in which adult fish are generally intolerant of other conspecifics other than their own mate (Kuwamura, 1986; Desjardins et al., 2008).

In order to better understand the behavioural building blocks of sociality, we investigated socially relevant behavior in two closely related lamprologine cichlids, *Neolamprologus pulcher* and *Telmatochromis temporalis* (Fig. 1). These two species split approximately 2 million years ago (Day et al., 2007; Sturmbauer et al., 2010), and continue to share a similar ecology, but have diverged dramatically in their social system. *Neolamprologus pulcher* are cooperative breeders that live in permanent social groups consisting of a single dominant breeding pair, and an average of 5–7 subordinate fish that act as helpers at the nest, assisting with brood care, territory maintenance and defence (Taborsky and Limberger, 1981; Taborsky, 1984; Balshine-Earn et al., 1998; Balshine et al., 2001; Heg et al., 2005; Wong and Balshine, 2011). These subordinate group members are often not closely related to the dominant breeding pair (Stiver et al., 2004, 2005; Hellmann et al., 2015a,b). In contrast, *T. temporalis* never form groups (Mboko and Kohda, 1999; Heg and Bachar, 2006). However, both species live in the same areas of the rocky littoral zone in Lake Tanganyika, and share similar habitat requirements and predation regimes (Kuwamura, 1986; Brichard, 1989; Konings, 1998). Furthermore, both cichlids are territorial substrate spawners with biparental care (Kuwamura, 1986). Both species are small bodied (<80 mm standard length), and readily adapt to the laboratory environment.

Using these two species (one group living, and one not), we measured and compared behaviours hypothesized to be building blocks of sociality (Soares et al., 2010). Using newly collected data from the laboratory and the field, we examined social motivation, the tendency to value interactions with conspecifics compared to other alternatives. Additionally, by reanalyzing previously published data, we examined conflict resolution tactics that are used to settle an agonistic interaction. We predicted that relative to the non-grouping *T. temporalis*, the group-living *N. pulcher* would display greater social motivation, and make greater use of submissive behaviour, a conflict resolution tactic that facilitates group formation and maintenance (Bergmüller and Taborsky, 2005). Through this set of studies, we hoped to gain insight into some of the basic behavioural building blocks that make up a highly social phenotype, and broaden our understanding of the evolution and maintenance of sociality.

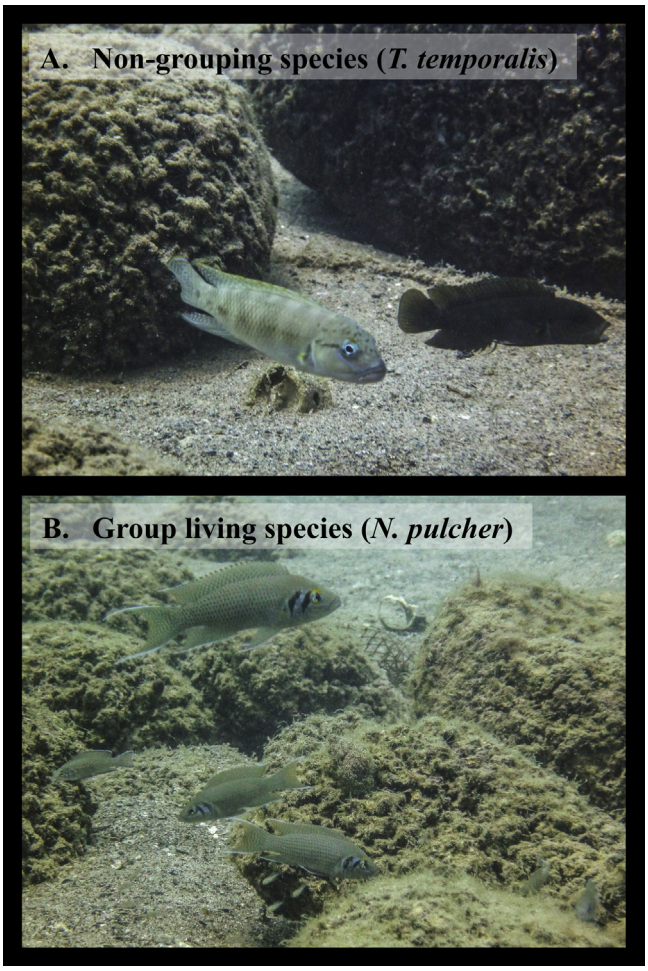

Fig. 1. (A) *Telmatochromis temporalis* and (B) *Neolamprologus pulcher* are two closely related Lamprologine cichlid fishes that are similar in body size, appearance, and ecology, but differ in social system. *Neolamprologus pulcher* are group living while *T. temporalis* non-grouping. Photo credits: Susan Marsh-Rollo and Jen Reynolds.

2. Methods

2.1. Measurement of social behaviour in the field

Field based behavioural studies were conducted at our long-term study site located at Kasakalawe Bay (8°46'52" S, 31°5'18" E) in Lake Tanganyika, Zambia. This site is characterized by mixture of sand and cobble substrate with a gentle descent to depth (for detailed descriptions of the study site, see Balshine-Earn et al., 1998; Balshine et al., 2001; Stiver et al., 2005; Bergmüller et al.,

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