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Habitat preferences depend on substrate quality in a cooperative breeder

Dario Josi, Michael Taborsky and Joachim G. Frommen

Department of Behavioural Ecology, Institute of Ecology and Evolution,
University of Bern, Hinterkappelen, Switzerland

ABSTRACT

Background: The evolution of complex social organization is mediated by diverse environmental constraints, including predation risk and the availability and distribution of food resources, mating partners, and breeding habitats. The cooperatively breeding cichlid *Neolamprologus pulcher* inhabits highly distinct habitats ranging from sheer rock faces to gastropod shells, rubble and sandy bottoms with dispersed stones. Physical habitat characteristics influence predator abundance and consequently the social system and reproductive performance of this species. Under natural conditions, habitat preferences should facilitate optimization of territorial position within a colony.

Question: When given the choice, does *N. pulcher* have a preference for environments differing in structural complexity and the presence of sand?

Method: We created breeding groups consisting of a dominant pair and two subordinates. We manipulated structural complexity (low vs. high stone cover) and sandy environments (present vs. absent). We measured habitat preference using a four-factorial design with binary choice options.

Predictions: We predicted that groups prefer to settle in a highly structured environment that provides many places to hide from potential predators. We further predicted a preference for a sandy bottom, especially in environments with low structural complexity, because sand allows shelters to be dug out.

Results and conclusion: *Neolamprologus pulcher* favoured more complex over less complex habitats, independently of the presence of sand. When fish faced low structural complexity in both experimental compartments, the presence of sand became a critical factor. Choosing appropriate habitats may help to reduce predation risk.

Keywords: cichlid, *Neolamprologus pulcher*, pay-to-stay, protection, shelter digging, territoriality.

Correspondence: D. Josi, Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, CH-3032 Switzerland. email: dario.josi@iee.unibe.ch

INTRODUCTION

The availability and distribution of resources, mating partners, and suitable breeding habitats has an effect on the social organization and mating system of many animals (Muller *et al.*, 1997; Hatchwell and Komdeur, 2000; Groenewoud *et al.*, 2016; for a review, see Rubenstein and Abbot, 2017). Throughout an animal's lifespan, the choice of an appropriate habitat is crucial in order to maximize survival and reproductive success. Within a particular habitat the micro-environment can be heterogeneous, and local resource competition might constrain life-history decisions (Hamilton and May, 1977; Emlen, 1982). For example, the limited availability of high-quality habitats might increase the benefits for offspring to remain philopatric (Komdeur *et al.*, 1995). Such a delay in dispersal favours the formation of complex social groups and the evolution of altruistic behaviour, as observed in cooperatively breeding species where subordinate individuals help to raise the offspring of dominants (Koenig *et al.*, 1992; Komdeur, 1992; Komdeur *et al.*, 1995).

In many fish species, the most important habitat characteristic is the availability of protective shelters to guard against predation (Hixon and Beets, 1993). This leads to high levels of intra- and interspecific competition for appropriately sized shelters. Substrate-breeding cichlids are among the best studied cave-breeding fish species (Balshine *et al.*, 2001; Thünken *et al.*, 2007; Tanaka *et al.*, 2015; Taborsky and Wong, 2017). In the habitats they occupy, they use a wide range of structures for hiding and breeding, ranging from holes and crevices in rocks to accumulations of empty gastropod shells and shelters dug out from sand or mud (Winkelmann *et al.*, 2014; Groenewoud *et al.*, 2016). Often, individuals excavate their shelters by removing sand and debris from underneath stones. The presence and extent of such movable material is especially relevant because it allows the environment to be modulated, allowing the size of the shelter entrance, for example, to be optimized (Dinh *et al.*, 2014; Taborsky and Wong, 2017). In contrast, in purely rocky habitats neither the number nor the size of shelters can be modified owing to the lack of material that can be manipulated. Hence, the presence of sand as well as the number and size of shelters influence survival and reproductive success (Balshine *et al.*, 2001; Tanaka *et al.*, 2018a). Accordingly, individuals should be choosy with respect to habitat quality. Such choosiness has, for example, been shown in the cichlid *Julidochromis transcriptus*, in which females preferred spawning substrate that allowed them to manipulate fertilization success of males, leading to increased levels of brood care by the putative fathers (Kohda *et al.*, 2009). In *Telmatochromis temporalis*, individuals generally favoured rocks over shells, but size-dependent competition compelled smaller individuals to use a shell habitat leading to restricted gene flow and potential reproductive isolation (Winkelmann *et al.*, 2014).

In cooperatively breeding fishes, where subordinate individuals support the dominant breeders by excavating cavities that serve as shelter and a breeding chamber (Taborsky, 1984; Tanaka *et al.*, 2018b), differences in substrate quality have the potential to shape the social organization of a group. For example, the need for subordinates to dig out the breeding cavity is absent in populations that live on purely rocky substrate (Groenewoud *et al.*, 2016). Despite these potential effects of habitat characteristics on social organization and important life-history decisions, experimental evidence for substrate preferences remains scarce (but see Eggleston and Lipcius, 1992; Taborsky *et al.*, 2014; Winkelmann *et al.*, 2014). Many cooperatively breeding cichlid species appear to specialize in habitats with limited substrate variation (Tanaka *et al.*, 2015; Taborsky and Wong, 2017). In contrast, the cooperatively breeding cichlid *Neolamprologus pulcher* inhabits a large variety of habitats, ranging from pure rocky bottoms to sandy stretches with dispersed stones and to accumulations of empty gastropod shells (Groenewoud *et al.*, 2016).

Neolamprologus pulcher is endemic to Lake Tanganyika, where it breeds in cooperative groups consisting of a dominant breeding pair and 1–25 immature and mature subordinates (Taborsky and Limberger, 1981; Heg *et al.*, 2005; Groenewoud *et al.*, 2016; Taborsky, 2016). Groups are organized in a size-based hierarchy where smaller individuals are submissive to larger ones, including the breeding pair (Taborsky, 1985, 2016). The sexes differ in their dispersal strategies, with males being more likely to disperse, while females tend to queue for breeding positions in their natal group (Dierkes *et al.*, 2005; Stiver *et al.*, 2006; Hellmann *et al.*, 2016). Within a group, individuals participate in territory defence against conspecifics and other species, including competitors for space and predators of eggs, young, and adults (Taborsky and Limberger, 1981; Heg and Taborsky, 2010; Bruintjes and Taborsky, 2011). Furthermore, they invest in territory maintenance by removing sand from underneath stones (Taborsky, 1984; Groenewoud *et al.*, 2016). These excavated cavities are of crucial importance as they serve as a haven from predators and as a breeding chamber for the dominant individuals. Digging behaviour is costly in terms of energy and time invested (Grantner and Taborsky, 1998), thus individuals only invest in digging within their home territory. Indeed, digging is a task that subordinates undertake in return for being allowed to remain in the dominant's territory (Bergmüller and Taborsky, 2005; Bergmüller *et al.*, 2005a; Zöttl *et al.*, 2013b). Thus, territory quality influences the need for assistance and, as a consequence, the social system of *N. pulcher* (Balshine *et al.*, 2001; Groenewoud *et al.*, 2016). Consequently, strong preferences should be expected in this species regarding where to establish a territory, which might occur either at places where a high number of suitable shelters are already available, or where the substrate would allow digging out such cavities. To date, however, the habitat preferences in *N. pulcher*, and more generally in cave-breeding fishes, are little understood (but see Kohda *et al.*, 2009).

The aim of this study was to elucidate habitat preferences of dominant and subordinate *N. pulcher* by giving them the opportunity to choose between habitats differing in structural complexity and in the presence of sand. We predicted that *N. pulcher* would prefer (1) more complex habitats offering more shelters than less structured habitats, and (2) sandy habitats allowing them to create shelters of their own, which ought to be especially important in less structured habitats.

METHODS

Study animals

We conducted the experiment between April and May 2013 at the Hasli Ethological Station in Hinterkappelen, Switzerland. We used laboratory-reared F1 and F2 offspring of *N. pulcher* caught in the wild at the southern tip of Lake Tanganyika, near Mpulungu in Zambia. They were kept in aggregations of 5–30 individuals in mixed-sex groups. Tanks contained 50–400 litres of water, depending on the number of individuals. Water temperature (27 ± 1°C) and a 13 hour light/11 hour dark cycle resembled natural conditions at Lake Tanganyika. The bottom of each storage tank was covered with a 2 cm layer of sand and did not contain any shelters to prevent animals from breeding. Several open, semi-opaque plastic bottles at the surface served as hiding places. The fish were fed with commercial flake food five times a week, and once a week with defrosted zooplankton. In total, 80 individuals (20 groups, each containing four individuals) were used in the study.

Experimental set-up

We used six identical experimental tanks, each 100 cm long × 40 cm wide × 50 cm high. Each tank was divided into two halves using an opaque grey plastic partition. The partition left a gap 5 cm long × 45 cm high close to the front of the tank, so that fish could switch between compartments (see Figs. 1 and 2). The water was cleaned and aerated by two biological filters, one in each compartment. The two compartments contained a different habitat, between which the focal fish could choose. In total, we used 102 stones with a surface of 144.9 ± 25.8 cm^2 (mean ± SD) to create four different habitats. First, we tested preferences for habitat complexity in the presence or absence of sand. Focal fish could choose between a compartment of high structural complexity equipped with 12 stones and a compartment with low structural complexity containing just two stones (see Fig. 1). In half of these trials, a 2 cm layer of sand (see Fig. 1) covered the bottom of both compartments; in the other half, the tank was bare of sand. Stones were spread out over the bottom of the tank, thereby creating potential shelters. Thus, we created a habitat that offered many potential shelters and a habitat that offered a single shelter composed of two stones. Second, we tested preferences for sandy substrates in little and highly structured habitats. Here, one compartment contained sand and the other contained no sand, while both compartments were equipped either with two stones or 12 stones (see Fig. 2).

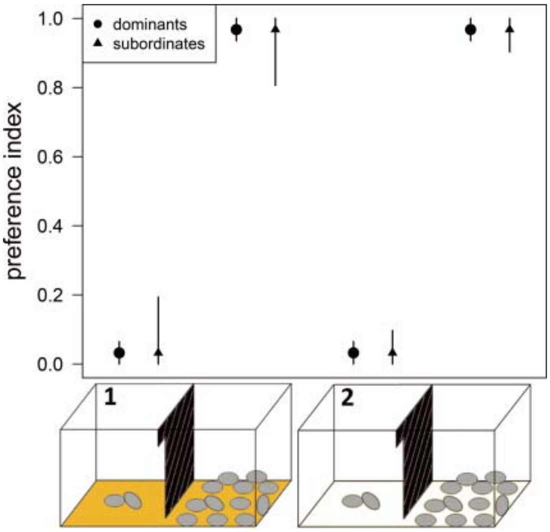

Fig. 1. *Preference for complex habitats.* When given the choice between habitats containing few or many stones, dominants and subordinates preferred the highly structured environment, independently of the presence (set-up 1) or absence (set-up 2) of sand. The preference index on the y-axis depicts the number of times individuals were observed in each compartment divided by the total counts obtained by scan sampling at 30 second intervals. Medians and interquartile ranges are shown for dominants and subordinates. Sketches on the abscissa depict the different habitats of set-up 1 and set-up 2.

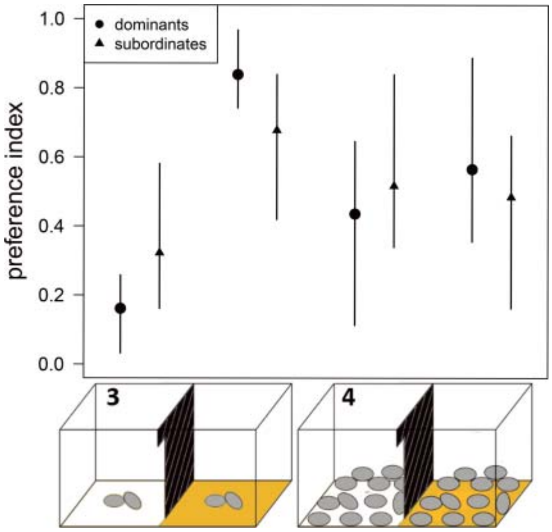

Fig. 2. *Preference for sandy habitats.* Dominants, but not subordinates, significantly preferred sandy habitats when overall structural complexity was low (set-up 3). When habitat complexity was high, there was no marked preference (set-up 4). The preference index on the y-axis depicts the number of times individuals were observed in each compartment divided by the total counts obtained by scan sampling at 30 second intervals. Medians and interquartile ranges are shown for dominants and subordinates. Sketches on the abscissa depict the different habitats of set-up 3 and set-up 4.

Experimental procedure

We examined four groups at the same time. One experimental run lasted 6 days. On the first day, a dominant male and a dominant female, as well as one large and one small subordinate individual, were caught from different storage tanks. The individuals of each group were unrelated and unfamiliar to each other to avoid any effects of familiarity or kinship (Le Vin *et al.*, 2010). After their capture, we measured the standard length (SL, accuracy ± 1 mm) of each fish. Dominant males (66 ± 5 mm; mean ± SD) of a pair were always larger than dominant females (59 ± 5 mm). Large subordinates (33 ± 2 mm) and small subordinates (26 ± 2 mm) were considerably smaller than the dominants to lower the potential for within-group conflict (Hamilton *et al.*, 2005).

At the beginning of each experimental run, we placed each group into a 50-litre aggregation tank for 2 days to accustom the fish to one another and to ensure group stability. Each tank contained two flowerpot halves and plastic bottles close to the water surface to curb aggressive interactions. We introduced the small subordinate first, followed by the large subordinate (30 minutes later) and then the dominant breeders (90 minutes later). After this group-establishment phase, the observational trials were commenced. On the first day, all individuals of a group were placed into the experimental tank in the same way as described above. Each fish was released by hand close to the gap in the partition in the middle of the tank.

To elucidate potential changes in preference for the different habitats over time, we observed the position of the fish three times within 24 hours. We measured their initial choice by recording the location of each individual every 30 seconds for 4 minutes starting

2 hours after the release of the last fish into the experimental tank. Each group of fish were then kept overnight in their respective set-up tank. The observation was continued the following morning, after 20 hours. This time, we noted the position of the fish every 30 seconds for 8 minutes, and observed dominants and subordinates sequentially. After 23 hours, the positions of all four fish were again recorded every 30 seconds for 4 minutes. Afterwards, all fish were fed and placed into a new tank containing the next set-up. The sequence of set-ups was chosen at random, and we took care that none of the 20 groups was tested in the same sequence. After a group was removed from a tank, all stones were cleaned with water and ethanol and a new habitat was constructed in that tank to avoid preference for a particular combination of stones or side effects. During the experiment, one large subordinate and 12 small subordinates were evicted from their groups, at least during some of the trials. These fish were prevented from getting close to the bottom of the tank (Zöttl *et al.*, 2013a) and were therefore excluded from the analyses.

Statistical analysis

We analysed the data with R v.3.1.1 (R Development Core Team, 2014) using the package 'lme4' (Bates *et al.*, 2013). We fitted generalized linear mixed-effect models (GLMM) or linear mixed-effect models (LMM). If models were over-dispersed (Bolker *et al.*, 2009), we included an individual-based random effect (Elston *et al.*, 2001). The significance of parameters was estimated based on likelihood ratio tests (LRT), assuming a χ^2-distribution.

In a first step, we tested for differences in preference between the observations after 2, 20, and 23 hours using an LMM. As the three different observations differed in duration, we calculated a preference ratio for each observation using the number of times each individual was observed in one compartment, divided by the total number of location recordings. We applied an arcsine square root transformation in order to archive normally distributed residuals. The respective preference ratios served as the response variable, and the three time points were included as a fixed factor. Additionally, we included status (dominant or subordinate) as a fixed factor and tested for an interaction between status and time. Non-significant interactions were removed from the final model. To account for different experimental set-ups and repeated measurements of the same group, we included *set-up ID* (i.e. the respective experimental set-up) and *group ID* (to account for the use of four individuals per group) as random effects. As there were no significant differences in preference between the 2, 20, and 23 hour observations (see Results), we combined the respective measurements for further analysis, resulting in a total of 31 measurements per individual.

To address our main question, we analysed positions within the respective set-ups. As the previous model revealed differences in the preference strength of dominants and subordinates (see Results), we proceeded by analysing data for dominants and subordinates independently. Therefore, we fitted two GLMMs (one for breeders, one for subordinates) for each of the four set-ups using a binomial error distribution. We used a proportional response variable including the number of times each individual was observed in each compartment. For the dominant breeder models, we included sex as a factor in order to elucidate differences between males and females. For the subordinate models, we included subordinate size class as an explanatory variable. We included *group ID* as a random effect in all these models to account for group membership. In these models, a significant intercept indicates that preference for a certain habitat differs from chance.

RESULTS

There was no significant difference in preference ratios between the 2, 20 and 23 hour observations ($\chi^2 = 2.017$, $df = 2$, $P = 0.36$). Overall, the preferences of subordinates were less pronounced than those of breeders ($\beta = -0.17 \pm 0.027$; $\chi^2 = 36.64$, $df = 1$, $P < 0.001$). These differences did not change significantly over time (time*status: $\chi^2 = 4.49$, $df = 1$, $P = 0.11$).

Dominants and subordinates preferred the highly structured habitat over the low structured habitat, independently of whether the set-up included sand or not (see Table 1; Fig. 1 set-ups 1 and 2). When keeping the structure constant in both compartments (see Fig. 2 set-ups 3 and 4), the presence of sand gained importance. If the habitats contained low structure, dominants – but not subordinates – preferred the side containing sand (see Table 1; Fig. 2 set-up 3). Finally, neither dominants nor subordinates showed a significant preference for sand when both compartments were highly structured (Table 1; Fig. 2 set-up 4). The sex of the dominants and subordinate size class had no significant effect on any of our model results (see Table 1).

Table 1. Model summaries of GLMMs showing parameter estimates of each experimental set-up for dominants and subordinates, including either sex (for dominants) or size class (for subordinates)

Set-up	Effects	Estimate ± SE	χ^2-value	*P*-value
Dominants				
Set-up 1	Intercept	3.375 ± 0.365		**<0.001**
	Sex	−0.363 ± 0.238	2.35	0.13
Set-up 2	Intercept	3.718 ± 0.409		**<0.001**
	Sex	−0.199 ± 0.283	0.497	0.48
Set-up 3	Intercept	2.213 ± 0.400		**<0.001**
	Sex	−0.649 ± 0.487	1.679	0.195
Set-up 4	Intercept	0.408 ± 0.444		0.36
	Sex	0.227 ± 0.404	0.311	0.58
Subordinates				
Set-up 1	Intercept	3.436 ± 0.639		**<0.001**
	Size class	0.170 ± 0.252	0.457	0.5
Set-up 2	Intercept	3.152 ± 0.473		**<0.001**
	Size class	0.203 ± 0.709	0.081	0.78
Set-up 3	Intercept	0.440 ± 0.302		0.15
	Size class	0.685 ± 0.400	3.038	*0.08*
Set-up 4	Intercept	−0.333 ± 0.435		0.44
	Size class	−0.324 ± 0.703	0.209	0.65

Note: In set-up 1, the compartments contained few or many rocks, with sand present in both compartments. Set-up 2 had the same structure but lacked sand in both compartments. Set-up 3 contained few rocks on both sides and sand in one of the compartments. Set-up 4 contained many rocks on both sides and sand in one of the compartments (cf. Figs. 1 and 2). Positive estimates for sex indicate stronger preferences on the part of males than females, while positive estimates for size class indicate stronger preferences on the part of smaller subordinates compared with larger ones. Statistically significant effects ($P < 0.05$) are shown in bold font and tendencies ($0.05 < P < 0.1$) in italics.

DISCUSSION

Habitat characteristics are important drivers of sociality in many animals, as they can influence group size and social complexity, among other parameters (Rubenstein and Abbot, 2017). In *N. pulcher*, choosing an appropriate habitat might drastically increase predator avoidance options and, consequently, the chances of survival. Accordingly, individuals should prefer habitats that offer protective shelters against predation. We show that dominants and subordinates of *N. pulcher* prefer highly structured habitats to those with low structure, independently of the presence of sand. Indeed, focal individuals spent almost all of their time in the highly structured habitat (Fig. 1). This choice was made quickly and consistently, as we could not detect any differences in preference between the 2, 20, and 23 hour observations. Additionally, there was no significant difference between dominant males and dominant females.

While rocky habitats provide shelters that are easily accessible, the number of shelters and their size cannot be altered. Such modification is possible, however, in habitats that contain both rocks and sand. Consequently, when the structural complexity of the habitat was overall low, the ability to modify existing shelters by excavating sand gained additional importance. Under such conditions, dominants preferred sandy substrates (Fig. 2 set-up 3). The ability to excavate shelters in such habitats may affect the number of group members and overall social structure (Balshine *et al.*, 2001). Indeed, a recent study showed that groups of *N. pulcher* in sandy habitats were larger (Groenewoud *et al.*, 2016). This effect was due to an increased number of small subordinates per group, which are heavily involved in habitat maintenance, including digging and substrate cleaning (Taborsky *et al.*, 1986; Heg and Taborsky, 2010; Groenewoud *et al.*, 2016). Our results also indicate that smaller helpers tend to be more readily tolerated in the sandy compartment of a low structured habitat than are large helpers (see Table 1; Fig. 2 set-up 3). Habitat choice has therefore the potential to influence the need for help, which can feed back on group size and group composition. However, in nature there might be trade-offs between habitat quality and other environmental factors leading to a change in habitat preference. For example, wolf spiders (*Pardosa milvina*) had a preference for more complex over bare substrates in predator-free environments, but showed altered preferences if predator cues were introduced (Rypstra *et al.*, 2007). In *N. pulcher*, competition over suitable, high-quality breeding sites plays an important role in shaping the social structure, as competition is directly correlated with group size, group persistence, offspring production, and anti-predator behaviour (Balshine *et al.*, 2001; Heg *et al.*, 2004, 2005; Jungwirth *et al.*, 2015b). Under natural conditions, intraspecific competition leads to the differential occupation of distinct micro-habitats in *N. pulcher* and other cichlid species (Heg *et al.*, 2008; Taborsky *et al.*, 2014; Winkelmann *et al.*, 2014). Such field observations are supported by our experimental data. Dominants and subordinates showed similar preferences for the highly structured habitat providing many shelters. This effect was different in overall less-structured habitats, where subordinates were less often found on the sandy side than breeders. Such a reduced preference on the part of subordinates compared with dominants might be explained by two non-mutually exclusive hypotheses. First, they could be the consequence of competition for access to shelters. If the structural complexity of a habitat is low, there are fewer hiding places to which not all individuals of a group have equal access. In the absence of predation risk, it could be advantageous for subordinates to switch to a suboptimal habitat instead of competing for access to shelters with dominants. Second, owing to a lack of predation risk in combination with access to unoccupied breeding substrate, subordinates might decide to disperse and occupy their own territory. Indeed, in many cooperative breeders the availability of safe breeding opportunities leads subordinate individuals to disperse (Pruett-Jones and Lewis, 1990; Komdeur, 1992; Walters *et al.*, 1992; Tanaka *et al.*, 2016), which has also been experimentally demonstrated in *N. pulcher*, both in the laboratory and in the field (Bergmüller *et al.*, 2005b; Hamilton *et al.*, 2005; Jungwirth *et al.*, 2015a). Whether the weaker preferences of subordinates for a given habitat in our study were driven by high levels of aggression among group members or the possibility to safely establish their own territories ought to be addressed in futures studies.

In summary, our results reveal habitat preferences in the territorial and cooperatively breeding cichlid *N. pulcher*. They indicate that a reduction in the availability of shelters increases the preference for sandy substrates, likely because these can be modified to increase their protective potential. In populations dwelling on sand, digging by subordinates may be an important means to increase their acceptance by more dominant individuals (Zöttl *et al.*, 2013b; Quiñones *et al.*, 2016). Substrate differences therefore have the potential to strongly influence the complex social structure of this species.

AUTHOR CONTRIBUTIONS

D.J., M.T., and J.G.F. planned the study. M.T. and J.G.F. organized funding. D.J. conducted the experiments and analysed the data. D.J., M.T., and J.G.F. discussed the results. D.J. and J.G.F. wrote the first draft of the manuscript, which M.T. edited. All authors read and approved the final version of the manuscript.

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