

1 **Habitat preferences depend on substrate quality in a cooperative**

2 **breeder**

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15 **Abstract**

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

23 **Question:** If given the choice, does *N. pulcher* distinguish between environments differing in
24 structural complexity and the presence of sand?

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

28 **Predictions:** We predicted that groups prefer to settle in a highly structured environment
29 providing many possibilities to hide from potential predators. We further predicted a preference for
30 sandy bottom, especially in environments with low structural complexity, because sand allows for
31 digging out shelters.

32 **Results and Conclusion:** *N. pulcher* favored more complex over less complex habitats,
33 independently of the presence of sand. When fish faced low structural complexity in both experimental
34 compartments, sand presence became a critical factor. Choosing appropriate habitats may contribute to
35 effectively reduce predation risk.

36 **Introduction**

37 The availability and distribution of resources, mating partners, and suitable breeding habitats affects the
38 social organization and mating system of many animals (Muller *et al.*, 1997; Hatchwell and Komdeur,
39 2000; Groenewoud *et al.*, 2016; for review see: Rubenstein and Abbot, 2017). Throughout an animal's
40 lifespan, the choice of an appropriate habitat is crucial in order to maximize survival and reproductive
41 success. Even within a certain habitat the microenvironment is often heterogeneous, and local resource
42 competition might constrain life history decisions (Hamilton and May, 1977; Emlen, 1982). For example,
43 the limited availability of high quality habitats might increase the benefits for offspring to remain
44 philopatric (Komdeur *et al.*, 1995). Such delay in dispersal favours the formation of complex social groups
45 and the evolution of altruistic behaviour, as observed in cooperatively breeding species where
46 subordinate individuals help raising offspring of dominants (Koenig *et al.*, 1992; Komdeur, 1992;
47 Komdeur *et al.*, 1995).

48 In many fish species, the most important habitat characteristic is the availability of protective shelters in
49 order to avoid predation (Hixon and Beets, 1993). This leads to high levels of intra- and interspecific
50 competition for appropriately sized shelters. Substrate breeding cichlids are among the best studied cave
51 breeding fish species (Balshine *et al.*, 2001; Thünken *et al.*, 2007; Tanaka *et al.*, 2015; Taborsky and
52 Wong, 2017). Within their habitats, they use a wide range of structures for hiding and breeding,
53 extending from holes and crevices in rocks to accumulations of empty gastropod shells and shelters dug
54 out from sand or mud (Winkelmann *et al.*, 2014; Groenewoud *et al.*, 2016). Often, individuals excavate
55 their shelters by removing sand and debris from underneath stones. The presence and extent of such
56 movable material is of particular relevance because it allows to modulate the environment, optimizing
57 for example the size of the shelter entrance (Dinh *et al.*, 2014; Taborsky and Wong, 2017). In contrast, in
58 purely rocky habitats neither the number nor the size of shelters can be modified due to the lack of
59 material that can be manipulated. Hence, the presence of sand as well as the number and size of shelters

60 influence survival and reproductive success (Balshine *et al.*, 2001; Tanaka *et al.*, 2018a). Accordingly,
61 individuals should be choosy with respect to habitat quality. Such choosiness has for example been
62 shown in the cichlid *Julidochromis transcriptus*, where females prefer spawning substrate that allow
63 them to manipulate fertilization success of males, leading to increased levels of brood care by the
64 putative fathers (Kohda *et al.*, 2009). In *Neolamprologus temporalis*, individuals generally favour rocks
65 over shells, but size dependent competition compelled smaller individuals to use a shell habitat leading
66 to restricted gene flow and potential reproductive isolation (Winkelman *et al.*, 2014).

67 In cooperatively breeding fishes, where subordinate individuals support the dominant breeders by
68 excavating cavities that serve as shelter and breeding chamber (Taborsky, 1984; Tanaka *et al.*, 2018b),
69 differences in substrate quality bear the potential to shape the social organisation of a group. For
70 example, the need for subordinates to dig out the breeding cavity is absent in populations that live on
71 purely rocky grounds (Groenewoud *et al.*, 2016). Despite these potential effects of habitat characteristics
72 on social organization and important life history decisions, experimental evidence for substrate
73 preferences is still scarce (but see: Eggleston and Lipcius, 1992; Taborsky *et al.*, 2014; Winkelman *et al.*,
74 2014). Many cooperatively breeding cichlid species appear to be specialized on habitats with limited
75 substrate variation (Tanaka *et al.*, 2015; Taborsky and Wong, 2017). In contrast, the cooperatively
76 breeding cichlid *Neolamprologus pulcher* inhabits a large variety of habitats, ranging from pure rocky
77 bottoms to sandy stretches with dispersed stones and to accumulations of empty gastropod shells
78 (Groenewoud *et al.*, 2016). *N. pulcher* is endemic to Lake Tanganyika, where it breeds in cooperative
79 groups consisting of a dominant breeding pair and 1 to 25 immature and mature subordinates (Taborsky
80 and Limberger, 1981; Heg *et al.*, 2005; Groenewoud *et al.*, 2016; Taborsky, 2016). Groups comprise a size
81 based hierarchy where smaller individuals are submissive to larger ones, including the breeding pair
82 (Taborsky, 1985, 2016). Sexes differ in their dispersal strategies, with males being more likely to disperse,
83 while females tend to queue for breeding positions in their natal group (Dierkes *et al.*, 2005; Stiver *et al.*,

84 2006; Hellmann *et al.*, 2016). Within a group, individuals participate in territory defence against
85 conspecifics and other species, including space competitors and predators of eggs, young and adults
86 (Taborsky and Limberger, 1981; Heg and Taborsky, 2010; Brintjes and Taborsky, 2011). Furthermore,
87 they invest in territory maintenance by removing sand underneath stones (Taborsky, 1984; Groenewoud
88 *et al.*, 2016). These excavated cavities are of crucial importance as they serve as a hide from predators
89 and as breeding chamber for the dominant individuals. Digging behaviour is costly in terms of energy and
90 time invested (Grantner and Taborsky, 1998), thus individuals only invest in digging within their home
91 territory. Indeed, digging is one way how subordinates pay to be allowed to stay in the dominant's
92 territory (Bergmüller and Taborsky, 2005; Bergmüller *et al.*, 2005a; Zöttl *et al.*, 2013b). Territory quality,
93 thus, influences the need of help and, as a consequence, the social system of *N. pulcher* (Balshine *et al.*,
94 2001; Groenewoud *et al.*, 2016). Consequently, strong preferences should occur in this species regarding
95 where to establish a territory, which might happen either at places where a high number of suitable
96 shelters is already present, or where the substrate would allow digging out such cavities. However, thus
97 far habitat preferences in *N. pulcher*, and more generally in cave breeding fishes, are little understood
98 (but see Kohda *et al.*, 2009).

99 The aim of this study was to elucidate habitat preferences of dominant and subordinate *N. pulcher* by
100 providing them the opportunity to choose between habitats differing in structural complexity and in the
101 presence of sand. We predicted that *N. pulcher* prefers (i) more complex habitats offering more shelters
102 than less structured habitats, and (ii) sandy habitats allowing them to create shelters of their own, which
103 should be especially important if the habitat is little structured.

104 **Methods**

105 *Study animals*

106 We conducted the experiment between April and May 2013 at the Ethological Station Hasli,
107 Hinterkappelen, Switzerland. We used laboratory-reared F1 and F2 offspring of *N. pulcher* caught in the
108 wild at the southern tip of Lake Tanganyika, near Mpulungu, Zambia. They were kept in aggregations of 5
109 - 30 individuals in mixed sex groups. Tanks contained 50 - 400 L of water, depending on the number of
110 individuals. Water temperature (27 ± 1 °C) and the light:dark cycle (of 13:11 hrs) resembled natural
111 conditions at Lake Tanganyika. The bottom of each storage tank was covered with a 2 cm sand layer and
112 did not contain any shelters to prevent animals from breeding. Several open, semi-opaque plastic bottles
113 at the surface served as hiding places. The fish were fed with commercial flake food five times a week,
114 and once a week with defrosted zooplankton. In total, 80 individuals (20 groups, each containing 4
115 individuals) were used in the study.

116 *Experimental set-up*

117 We used six identical experimental tanks, each measuring 100 x 40 x 50 cm (l x b x h). Each tank was
118 divided into two equal sized halves using an opaque grey plastic partition. The partition left a gap of 5 x
119 45 cm (l x h) close to the front of the tank, so that fish could switch between compartments (see Fig. 1
120 and 2). The water was cleaned and aerated by two biological filters, one in each compartment. Each
121 compartment contained a different habitat, between which the focal fish could choose. In total, we used
122 102 stones (stone surface (mean \pm S.D.): 144.9 ± 25.8 cm²) to create four different habitats. First, we
123 tested preferences for habitat complexity in the presence or absence of sand. Focal fish could choose
124 between a compartment of high structural complexity equipped with 12 stones and a compartment with
125 low structural complexity containing two stones (see Fig. 1). In half of these trials, a 2 cm layer of sand
126 (see Fig. 1) covered the bottom of both compartments, whereas the tank was bare of sand in the other
127 trials. Stones were spread out over the bottom of the tank, thereby creating potential shelters. Thus, we

128 created a habitat offering many potential shelters and a habitat offering only one shelter composed of
129 two stones. Second, we tested preferences for sandy substrates in little and highly structured habitats.
130 Here, one compartment contained sand and the other contained no sand, while both compartments
131 were either equipped with 2 stones or 12 stones (see Fig. 2).

132 *Experimental procedure*

133 We examined four groups at the same time. One experimental run lasted 6 days. On the first day, a
134 dominant male and a dominant female, as well as a large and a small subordinate individual, were
135 caught from different storage tanks. Individuals of each group were unrelated and unfamiliar to each
136 other to avoid any effects of familiarity or kinship (Le Vin *et al.*, 2010). After catching, the standard
137 length (SL, accuracy ± 1 mm) was measured. Dominant males (mean \pm S.D.: 66 ± 5 mm) of a pair were
138 always larger than dominant females (59 ± 5 mm). Large subordinates (33 ± 2 mm) and small
139 subordinates (26 ± 2 mm) were considerably smaller than the dominants to lower the potential for
140 within group conflict (Hamilton *et al.*, 2005).

141 At the beginning of each experimental run we placed each group into a 50 L aggregation tank for 2 days
142 to customize the fish to each other and to ensure group stability. Each tank contained two flowerpot
143 halves and plastic bottles close to the water surface to curb aggressive interactions. We introduced the
144 small subordinate first, followed by the large subordinate (30 minutes later) and the dominant breeders
145 (90 minutes later). After this group-establishing phase, the observational trials started. On the first day,
146 all individuals of a group were placed into the experimental tank in the same way as described above.
147 Each fish was released by hand close to the gap in the partition in the middle of the tank.

148 To elucidate potential changes in preferences for the different habitats over time, we observed the
149 position of the fish three times within 24 hours. We measured the early choice by recording the location
150 of each individual every 30 seconds for four minutes starting two hours after the release of the last fish
151 into the experimental tank. Afterwards, the groups were kept overnight in the respective set-up tank.

152 The observation was continued the following morning, after 20 hours. We noted down the position of
153 the fish every 30 seconds for 8 minutes. Here, we observed dominants and subordinates sequentially.
154 After 23 hours, the positions of all fish were recorded again for 4 minutes every 30 seconds. Afterwards,
155 all fish were fed and placed into a new tank containing the next set-up. The sequence of set-ups was
156 chosen randomly, and we took care that none of the 20 groups was tested in the same sequence. After a
157 group was removed from a tank, all stones were cleaned with water and ethanol and a new habitat was
158 constructed in each tank to avoid preference for a particular combination of stones or side effects.
159 During the experiment, one large subordinate and 12 small subordinates were evicted from their groups,
160 at least during some of the trials. These fish were not allowed to be close to the bottom of the tank (Zöttl
161 *et al.*, 2013a) and they were therefore excluded from the analyses of the respective trial.

162 *Statistical analysis*

163 We analysed the data in R 3.1.1 (R Core Team, 2014) using the package 'lme4' (Bates *et al.*, 2013). We
164 fitted generalized linear mixed-effect models (GLMM), or linear mixed-effect models (LMM). If models
165 were over-dispersed (Bolker *et al.*, 2009), we included an individual-based random effect (Elston *et al.*,
166 2001). The significance of parameters was estimated based on likelihood ratio tests (LRT), assuming a
167 χ^2 -distribution.

168 In a first step, we tested for preference differences between the observation after 2h, 20h and 23h using
169 a LMM. As the three different observations differed in time span, we calculated a preference ratio for
170 each observation using the number of times each individual was observed in one compartment, divided
171 by the total amount of location recordings. We applied an arcsine square root transformation in order to
172 archive normally distributed residuals. The respective preference ratios served as response variable, and
173 the three time points were included as a fixed factor. Additionally, we included status (dominant or
174 subordinate) as fixed factor and tested for an interaction between status and time. Non-significant
175 interactions were removed from the final model. To account for different experimental set-ups and

176 repeated measurements of the same group, we included *set-up ID* (that is the respective experimental
177 set-up), and *group ID* (to account for the use of four individuals per group) as random effects. As there
178 were no significant differences in preference between the 2h, 20h and 23h observation (see Results), we
179 combined the respective measurements for further analysis, resulting in a total of 31 measurements per
180 individual.

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

191 **Results**

192 There was no significant difference in preference ratios between the 2h, 20h and 23h observations
193 (Df=2, $\chi^2=2.017$, $p=0.36$). Overall, preferences in subordinates were less pronounced compared to
194 breeders ($\beta=-0.17\pm 0.027$, Df=1, $\chi^2=36.64$, $p<0.001$). These differences did not change significantly over
195 time (time*status, Df=1, $\chi^2=4.49$, $p=0.11$).

196 Dominants and subordinates preferred the highly structured habitat over the low structured habitat,
197 independently of whether the set-up was equipped with or without sand (see Table 1; Fig. 1: set-up 1
198 and 2). When keeping the structure constant in both compartments (see Fig. 2, set-up 3 and 4), the

199 presence of sand gained importance. If the habitats contained low structure, dominants, but not
200 subordinates, preferred the side containing sand (see Table 1; Fig. 2 set-up 3). Finally, neither dominants
201 nor subordinates showed significant preferences for sand when structure was high on both sides (Table
202 1; Fig. 2 set-up 4). The sex of the dominants and subordinate size class had no significant effect on any of
203 our model results (see Table 1).

204 **Discussion**

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

215 While rocky habitats provide shelters that are easily accessible, shelter number and size cannot be
216 modified. Such modification is possible in habitats containing rocks and sand. Consequently, when the
217 structural complexity was overall low, the possibility to modify the existing shelters by removing sand
218 gained additional importance. Under such conditions, dominants preferred sandy substrates (Fig. 2,
219 set-up 3). The need to dig out shelters in such habitats may affect the number of group members and
220 overall social structure (Balshine *et al.*, 2001). Indeed, a recent study showed that groups of *N. pulcher* in
221 sandy habitats were larger (Groenewoud *et al.*, 2016). This effect was due to an increased number of

222 small subordinates per group, which are strongly involved in habitat maintenance, including digging and
223 substrate cleaning (Taborsky *et al.*, 1986; Heg and Taborsky, 2010; Groenewoud *et al.*, 2016). Our results
224 also indicate that smaller helpers tend to be more readily tolerated in the sandy compartment of a low
225 structured habitat compared to large helpers (see Table 1; Fig. 2 set-up 3). Habitat choice has therefore
226 the potential to influence the need for help, which can feed back on group size and group composition.
227 However, in nature there might be trade-offs between habitat quality and other environmental factors
228 leading to a change in habitat preferences. For example, wolf spiders (*Pardosa milvina*) show a
229 preference for more complex over bare substrates in predator-free environments, but showed altered
230 preferences if predator cues were given (Rypstra *et al.*, 2007). In *N. pulcher*, competition over suitable,
231 high quality breeding sites plays an important role in shaping the social structure, as competition is
232 directly correlated with group size, group persistence, offspring production, and antipredator behaviour
233 (Balshine *et al.*, 2001; Heg *et al.*, 2004, 2005; Jungwirth *et al.*, 2015b). Under natural conditions,
234 intraspecific competition leads to the differential occupation of distinct micro-habitats in *N. pulcher* and
235 other cichlid species (Heg *et al.*, 2008; Taborsky *et al.*, 2014; Winkelmann *et al.*, 2014). Such field
236 observations are supported by our experimental data. Preferences for the highly structured habitat
237 providing many shelters were comparable for dominants and subordinates. This effect was different in
238 overall less structured habitats, where subordinates were less often found on the sandy side than
239 breeders. Such a reduced preference of subordinates compared to dominants might be explained by two
240 non-mutually exclusive hypotheses: First, they could be the consequence of competition for access to
241 shelters. If the structural complexity of a habitat is low, there are fewer hiding places and the space for
242 protection is limited and not equally accessible for all individuals of a group. In the absence of predation
243 risk, it could be advantageous for subordinates to switch to a suboptimal habitat instead of competing
244 for access to shelters with dominants. Second, due to a lack of predation risk in combination with access
245 to unoccupied breeding substrate subordinates might decide to disperse and occupy an own territory.
246 Indeed, in many cooperative breeders the availability of safe breeding opportunities leads subordinate

247 individuals to disperse (Pruett-Jones and Lewis, 1990; Komdeur, 1992; Walters *et al.*, 1992; Tanaka *et al.*,
248 2016), which has also been experimentally demonstrated in *N. pulcher*, both in the laboratory and field
249 (Bergmüller *et al.*, 2005b; Hamilton *et al.*, 2005; Jungwirth *et al.*, 2015a). Whether the weaker
250 preferences of subordinates for a given habitat in our study were driven by high levels of aggression
251 among group members or the possibility to safely establish own territories might be determined in
252 futures studies.

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

259 **Author's contributions**

260 DJ, MT and JGF planned the study. MT and JGF organized funding. DJ conducted the experiments and
261 analysed the data. DJ, MT and JGF discussed the results. DJ and JGF wrote the first draft of the
262 manuscript, which MT edited. All authors read and approved the final version of the manuscript.

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269 **References**

- 270 Balshine, S., Leach, B., Francis, N., Hannah, R., Taborsky, M. and Werner, N. 2001. Correlates of group
271 size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). *Behavioral Ecology and*
272 *Sociobiology*, **50**: 134–140.
- 273 Bates, D., Maechler, M. and Bolker, B. 2013. lme4: Linear mixed-effects models using S4 classes. *R*
274 *package version 1.1-7.*, See <https://cran.r-project.org/web/packages/lme4/>.
- 275 Bergmüller, R. and Taborsky, M. 2005. Experimental manipulation of helping in a cooperative breeder:
276 helpers ‘pay to stay’ by pre-emptive appeasement. *Animal Behaviour*, **69**: 19–28.
- 277 Bergmüller, R., Heg, D. and Taborsky, M. 2005a. Helpers in a cooperatively breeding cichlid stay and pay
278 or disperse and breed, depending on ecological constraints. *Proceedings of the Royal Society B*, **272**:
279 325–331.
- 280 Bergmüller, R., Heg, D., Peer, K. and Taborsky, M. 2005b. Extended safe havens and between-group
281 dispersal of helpers in a cooperatively breeding cichlid. *Behaviour*, **142**: 1643–1667.
- 282 Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., *et al.* 2009.
283 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and*
284 *Evolution*, **24**: 127–135.
- 285 Brintjes, R. and Taborsky, M. 2011. Size-dependent task specialization in a cooperative cichlid in
286 response to experimental variation of demand. *Animal Behaviour*, **81**: 387–394.
- 287 Dierkes, P., Heg, D., Taborsky, M., Skubic, E. and Achmann, R. 2005. Genetic relatedness in groups is
288 sex-specific and declines with age of helpers in a cooperatively breeding cichlid. *Ecology Letters*, **8**:
289 968–975.
- 290 Dinh, Q.M., Qin, J.G., Dittmann, S. and Tran, D.D. 2014. Burrow morphology and utilization of the goby
291 (*Parapocryptes serperaster*) in the Mekong Delta, Vietnam. *Ichthyological Research*, **61**: 332–340.
- 292 Eggleston, D.B. and Lipcius, R.N. 1992. Shelter selection by spiny lobster under variable predation risk,
293 social conditions, and shelter size. *Ecology*, **73**: 992–1011.

294 Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C. and Lambin, X. 2001. Analysis of aggregation, a
295 worked example: numbers of ticks on red grouse chicks. *Parasitology*, **122**: 563–569.

296 Emlen, S. 1982. The evolution of helping. I. An ecological constraints model. *The American Naturalist*,
297 **119**: 29–39.

298 Grantner, A. and Taborsky, M. 1998. The metabolic rates associated with resting, and with the
299 performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus*
300 *pulcher* (Pisces: Cichlidae). *Journal of Comparative Physiology - B Biochemical, Systemic, and*
301 *Environmental Physiology*, **168**: 427–433.

302 Groenewoud, F., Frommen, J.G., Josi, D., Tanaka, H., Jungwirth, A. and Taborsky, M. 2016. Predation risk
303 drives social complexity in cooperative breeders. *Proceedings of the National Academy of Science of*
304 *the U.S.A.*, **113**: 4104–4109.

305 Hamilton, I., Heg, D. and Bender, N. 2005. Size differences within a dominance hierarchy influence
306 conflict and help in a cooperatively breeding cichlid. *Behaviour*, **142**: 1591–1613.

307 Hamilton, W.D. and May, R.M. 1977. Dispersal in stable habitats. *Nature*, **269**: 578–581.

308 Hatchwell, B.J. and Komdeur, J. 2000. Ecological constraints, life history traits and the evolution of
309 cooperative breeding. *Animal Behaviour*, **59**: 1079–1086.

310 Heg, D. and Taborsky, M. 2010. Helper response to experimentally manipulated predation risk in the
311 cooperatively breeding cichlid *Neolamprologus pulcher*. *PLoS ONE*, **5**: e10784.

312 Heg, D., Bachar, Z., Brouwer, L. and Taborsky, M. 2004. Predation risk is an ecological constraint for
313 helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society B*, **271**:
314 2367–2374.

315 Heg, D., Brouwer, L., Bachar, Z. and Taborsky, M. 2005. Large group size yields group stability in the
316 cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*, **142**: 1615–1641.

317 Heg, D., Heg-Bachar, Z., Brouwer, L. and Taborsky, M. 2008. Experimentally induced helper dispersal in
318 colonially breeding cooperative cichlids. *Environmental Biology of Fishes*, **83**: 191–206.

319 Hellmann, J.K., Sovic, M.G., Gibbs, H.L., Reddon, A.R., O'Connor, C.M., Ligocki, I.Y., *et al.* 2016.
320 Within-group relatedness is correlated with colony-level social structure and reproductive sharing
321 in a social fish. *Molecular Ecology*, **25**: 4001–4013.

322 Hixon, M.A. and Beets, J.P. 1993. Predation, prey refuges, and the structure of coral-reef fish
323 assemblages. *Ecological Monographs*, **63**: 77–101.

324 Jungwirth, A., Josi, D., Walker, J. and Taborsky, M. 2015a. Benefits of coloniality: communal defence
325 saves anti-predator effort in cooperative breeders. *Functional Ecology*, **29**: 1218–1224.

326 Jungwirth, A., Walker, J. and Taborsky, M. 2015b. Prospecting precedes dispersal and increases survival
327 chances in cooperatively breeding cichlids. *Animal Behaviour*, **106**: 107–114.

328 Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L. and Stanback, M.T. 1992. The evolution of
329 delayed dispersal in cooperative breeders. *The Quarterly Review of Biology*, **67**: 111–150.

330 Kohda, M., Heg, D., Makino, Y., Takeyama, T., Shibata, J., Watanabe, K., *et al.* 2009. Living on the wedge:
331 female control of paternity in a cooperatively polyandrous cichlid. *Proceedings of the Royal Society*
332 *B*, **276**: 4207–4214.

333 Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative
334 breeding in the Seychelles warbler. *Nature*, **358**: 493–495.

335 Komdeur, J., Huffstadt, A., Prast, W. and Castle, G. 1995. Transfer experiments of Seychelles warblers to
336 new islands: changes in dispersal and helping behaviour. *Animal Behaviour*, **49**: 695–708.

337 Le Vin, A.L., Mable, B.K. and Arnold, K.E. 2010. Kin recognition via phenotype matching in a cooperatively
338 breeding cichlid, *Neolamprologus pulcher*. *Animal Behaviour*, **79**: 1109–1114.

339 Muller, K.L., Stamps, J.A., Krishnan, V. V and Willits, N.H. 1997. The effects of conspecific attraction and
340 habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *The American Naturalist*,
341 **150**: 650–661.

342 Pruett-Jones, S.G. and Lewis, M.J. 1990. Sex ratio and habitat limitation promote delayed dispersal in
343 superb fairy-wrens. *Nature*, **348**: 541–542.

344 Quiñones, A.E., van Doorn, G.S., Pen, I., Weissing, F.J. and Taborsky, M. 2016. Negotiation and
345 appeasement can be more effective drivers of sociality than kin selection. *Philosophical*
346 *Transactions of the Royal Society B*, **371**: 20150089.

347 R Core Team. 2014. R: A language and environment for statistical computing. *R Foundation for Statistical*
348 *Computing, Vienna, Austria*, URL <http://www.R-project.org/>.

349 Rubenstein, D.R. and Abbot, P. 2017. *Comparative social evolution* (D. R. Rubenstein and P. Abbot, eds).
350 Cambridge: Cambridge University Press.

351 Rypstra, A.L., Schmidt, J.M., Reif, B.D., DeVito, J. and Persons, M.H. 2007. Tradeoffs involved in site
352 selection and foraging in a wolf spider: effects of substrate structure and predation risk. *Oikos*, **116**:
353 853–863.

354 Stiver, K., Fitzpatrick, J., Desjardins, J. and Balshine, S. 2006. Sex differences in rates of territory joining
355 and inheritance in a cooperatively breeding cichlid fish. *Animal Behaviour*, **71**: 449–456.

356 Taborsky, B., Guyer, L. and Demus, P. 2014. “Prudent habitat choice”: a novel mechanism of
357 size-assortative mating. *Journal of Evolutionary Biology*, **27**: 1217–1228.

358 Taborsky, M. 1984. Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits.
359 *Animal Behaviour*, **32**: 1236–1252.

360 Taborsky, M. 1985. Breeder-helper conflict in a cichlid fish with broodcare helpers: An experimental
361 analysis. *Behaviour*, **95**: 45–75.

362 Taborsky, M. 2016. Cichlid fishes: a model for the integrative study of social behavior. In: *Cooperative*
363 *breeding* (W. D. Koenig and J. L. Dickinson, eds), pp. 272–293. Cambridge: Cambridge University
364 Press.

365 Taborsky, M. and Limberger, D. 1981. Helpers in fish. *Behavioral Ecology and Sociobiology*, **8**: 143–145.

366 Taborsky, M. and Wong, M. 2017. *Comparative social evolution* (D. R. Rubenstein and P. Abbot, eds).
367 Cambridge: Cambridge University Press.

368 Taborsky, M., Heart, E., von Siemens, M. and Stoerig, P. 1986. Social behaviour of *Lamprologus* species:

369 functions and mechanisms. *Annales de Musée Royal de l'Afrique Centrale, Sciences Zoologiques*,
370 **251**: 7–12.

371 Tanaka, H., Frommen, J.G. and Kohda, M. 2018a. Helpers increase food abundance in the territory of a
372 cooperatively breeding fish. *Behavioral Ecology and Sociobiology*, **72**: 51.

373 Tanaka, H., Frommen, J.G., Takahashi, T. and Kohda, M. 2016. Predation risk promotes delayed dispersal
374 in the cooperative breeding cichlid *Neolamprologus obscurus*. *Animal Behaviour*, **117**: 51–58.

375 Tanaka, H., Frommen, J.G., Engqvist, L. and Kohda, M. 2018b. Task-dependent workload adjustment of
376 female breeders in a cooperatively breeding fish. *Behavioral Ecology*, **29**: 221–229.

377 Tanaka, H., Heg, D., Takeshima, H., Takeyama, T., Awata, S., Nishida, M., *et al.* 2015. Group composition,
378 relatedness, and dispersal in the cooperatively breeding cichlid *Neolamprologus obscurus*.
379 *Behavioral Ecology and Sociobiology*, **69**: 169–181.

380 Thünken, T., Bakker, T.C.M., Baldauf, S.A. and Kullmann, H. 2007. Active inbreeding in a cichlid fish and
381 its adaptive significance. *Current Biology*, **17**: 225–229.

382 Walters, J.R., Copeyon, C.K. and Carter, J.H. 1992. Test of the ecological basis of cooperative breeding in
383 red- cockaded woodpeckers. *Auk*, **109**: 90–97.

384 Winkelmann, K., Genner, M., Takahashi, T. and Rüber, L. 2014. Competition-driven speciation in cichlid
385 fish. *Nature Communications*, **5**: 3412.

386 Zöttl, M., Frommen, J.G. and Taborsky, M. 2013a. Group size adjustment to ecological demand in a
387 cooperative breeder. *Proceedings of the Royal Society B*, **280**: 20122772.

388 Zöttl, M., Heg, D., Chervet, N. and Taborsky, M. 2013b. Kinship reduces alloparental care in cooperative
389 cichlids where helpers pay-to-stay. *Nature Communications*, **4**: 1341.

390 **Figures**

391 *Figure 1: Preference for complex habitats*

392 When given the choice between habitats containing few or many stones, dominants and subordinates
393 preferred the highly structured environment, independently of the presence (set-up 1) or absence (set-

394 up 2) of sand. The preference index on the y-axis depicts the number of times individuals have been
395 observed in each compartment divided by the total counts obtained by scan sampling at 30 s intervals.
396 Medians and interquartile ranges are shown for dominants and subordinates. Sketches on the abscissa
397 depict the different habitats of set-up 1 and set-up 2.

398 *Figure 2: Preference for sandy habitats*

399 Dominants, but not subordinates, preferred sandy habitats when overall structural complexity was low
400 (set-up 3). When habitat complexity was high, there was no significant preference (set-up 4). Preference
401 index at the y-axis depicts the number of times individuals have been observed in each compartment
402 divided by the total counts obtained by scan sampling at 30 s intervals. Medians and interquartile ranges
403 are shown for dominants and subordinates. Sketches on the abscissa depict the different habitats of
404 set-up 3 and set-up 4.

405 **Tables**

406 *Table 1:*

407 Model summaries of GLMMs showing parameter estimates of each experimental set-up for dominants
408 and subordinates, including either sex (for dominants) or size class (for subordinates). In set-up 1, the
409 compartments contained few or many rocks, with sand present in both compartments. Set-up 2 had the
410 same structure but lacked sand in both compartments. Set-up 3 contained few rocks on both sides and
411 sand in one of the compartments. Set-up 4 contained many rocks on both sides and sand in one of the
412 compartments (cf. Figures 1 and 2). Positive estimates for sex would indicate stronger preferences in
413 males compared to females and positive estimates for size class would indicate stronger preferences in
414 smaller helpers compared to larger helpers. Statistically significant effects ($p < 0.05$) are printed in bold
415 font and tendencies ($0.05 < p < 0.1$) in italics.

set-up	effects	estimate ± SE	χ^2 -value	p-value
<i>Dominants</i>				
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
<i>Subordinates</i>				
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

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Figure 1

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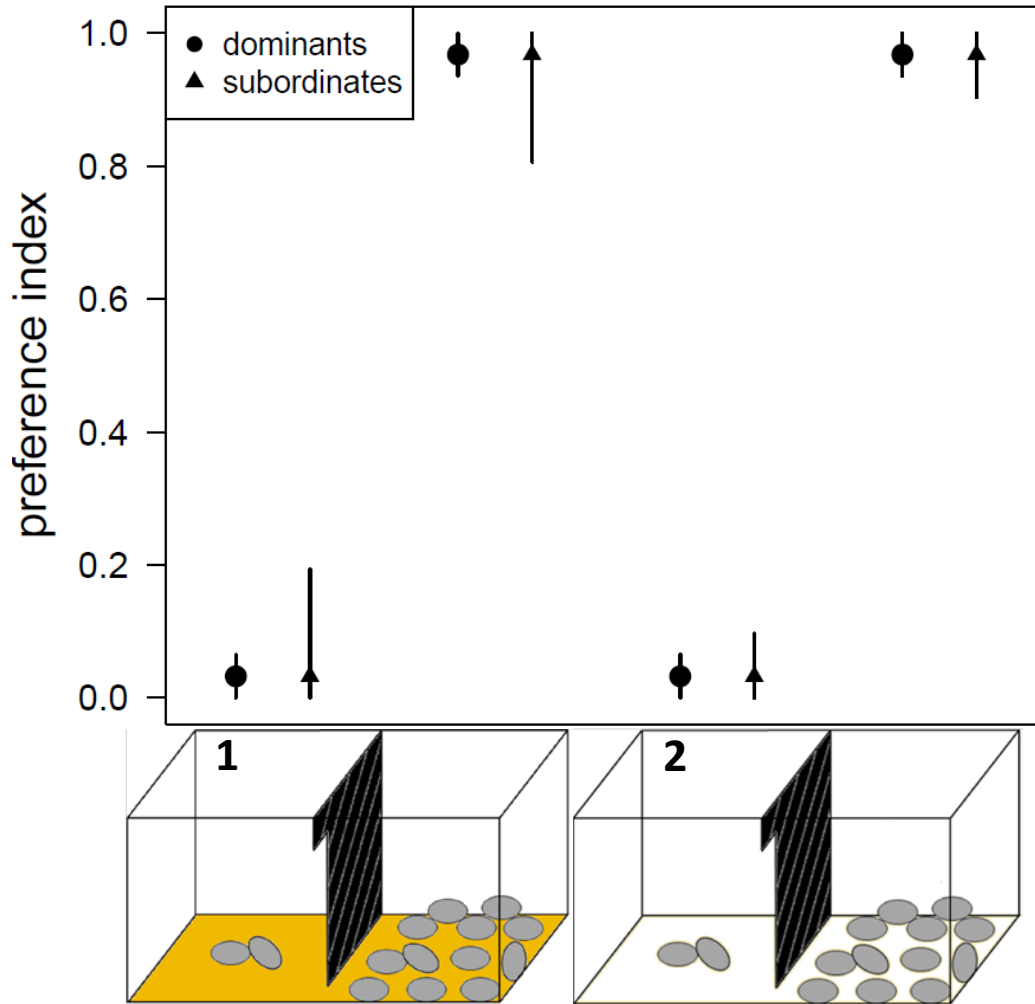
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430 **Figure 2**

