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# Predation risk drives social complexity in cooperative breeders

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**Predation risk is a major ecological factor selecting for group living. It is largely ignored, however, as an evolutionary driver of social complexity and cooperative breeding, which is attributed mainly to a combination of habitat saturation and enhanced relatedness levels. Social cichlids neither suffer from habitat saturation, nor are their groups composed primarily of relatives. This demands alternative ecological explanations for the evolution of advanced social organization. To address this question, we compared the ecology of eight populations of *Neolamprologus pulcher*, a cichlid fish arguably representing the pinnacle of social evolution in poikilothermic vertebrates. Results show that variation in social organization and behavior of these fish is primarily explained by predation risk and related ecological factors. Remarkably, ecology affects group structure more strongly than group size, with predation inversely affecting small and large group members. High predation and shelter limitation leads to groups containing few small but many large members, which is an effect enhanced at low population densities. Apparently, enhanced safety from predators by cooperative defense and shelter construction are the primary benefits of sociality. This finding suggests that predation risk can be fundamental for the transition toward complex social organization, which is generally undervalued.**

social evolution | social complexity | predation risk | ecological constraints | cooperative breeding

**P**redation risk is a key ecological factor selecting for adaptive responses in morphology, behavior, and life history decisions in animals (1, 2). In particular, it constitutes a fundamental selective force for group living (3, 4). Group members benefit from predator dilution or confusion (3, 5) and from joint effort in antipredator behavior, such as mobbing and vigilance (2). However, living in groups also entails costs; thus, group living should only evolve when, on average, the benefits of group living exceed its costs (4).

Long-term, stable groups mainly form in the context of reproduction. The most highly structured and complex groups occur when offspring are raised cooperatively, which often involves division of labor between group members (6, 7). In such cooperative groups, sexually mature individuals typically refrain from reproduction to raise the offspring of others (8–10), which may involve lifetime reproductive sacrifice (eusociality). The evolution of cooperative breeding is generally understood as a two-step process, where delayed dispersal is accompanied by the decision to provide alloparental brood care to dependent young (11). Limited dispersal resulting from habitat saturation may facilitate the evolution of cooperation by kin selection through the creation of kin neighborhoods (12). Empirical evidence is provided by correlations between relatedness and helping effort (13–15), and by interspecific correlations between monogamous mating and the incidence of cooperative breeding and eusociality (16, 17). However, this paradigm has limited explanatory power where habitats are not saturated and where cooperation

occurs between unrelated individuals, demanding alternative explanations to account for the evolution of complex social organization (18). Despite its central role in group formation, predation risk has rarely been recognized as an evolutionary force in the transition from simple to complex social organization, where subordinate nonbreeders provide alloparental care. This represents an important gap in our understanding of the evolution of complex social organization. It should be noted that the term “social complexity” has different connotations, especially when used in connection with different taxa, but there seems to be consensus that social complexity is not merely synonymous with group size. Instead, this term typically refers to social systems incorporating different types (or roles) of individuals within groups, accounting also for the nature and diversity of interactions among these individuals (19–21). Here, we demonstrate that variation in predation risk between populations can explain social organization and complexity in cooperatively breeding fish.

Predation risk may affect delayed dispersal, and hence group formation, in two possible ways. First, it increases the costs of dispersal by causing mortality when individuals disperse from their natal area to unfamiliar territory (22). This effect can be exacerbated when individuals need to sample their environment for suitable dispersal options (23, 24), as is the case in cooperative breeders keeping their territories all year round (25). Second, predation may render independent breeding unprofitable or impossible if the joint effort of group members is required for successful reproduction (2, 26, 27). Hence, predation risk is an important

## Significance

**It is widely accepted that high predation risk may select for group living, but predation is not regarded as a primary driver of social complexity. This view neglects the important effect of predation on dispersal and offspring survival, which may require cooperation among group members. The significance of predation for the evolution of social complexity can be well illustrated by behavioral and morphological adaptations of highly social animals showing division of labor, such as eusocial insects and cooperatively breeding fishes. By examining the diversity of social organization in a cooperative cichlid in relation to ecological variation, we show that predation risk has the greatest explanatory power of social complexity. This stresses the significance of predation for social evolution.**

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ecological constraint selecting for reduced or delayed dispersal, fulfilling two of three conditions (see conditions *ii* and *iii* below) proposed by the ecological constraints hypothesis (28). This hypothesis predicts delayed dispersal when there is: (*i*) a shortage of vacant breeding territories or mates, (*ii*) high mortality risk during dispersal, and (*iii*) a low chance of independent reproduction when a breeding territory has been established. These effects may be additive and can cause strong selection for delayed dispersal under high levels of predation.

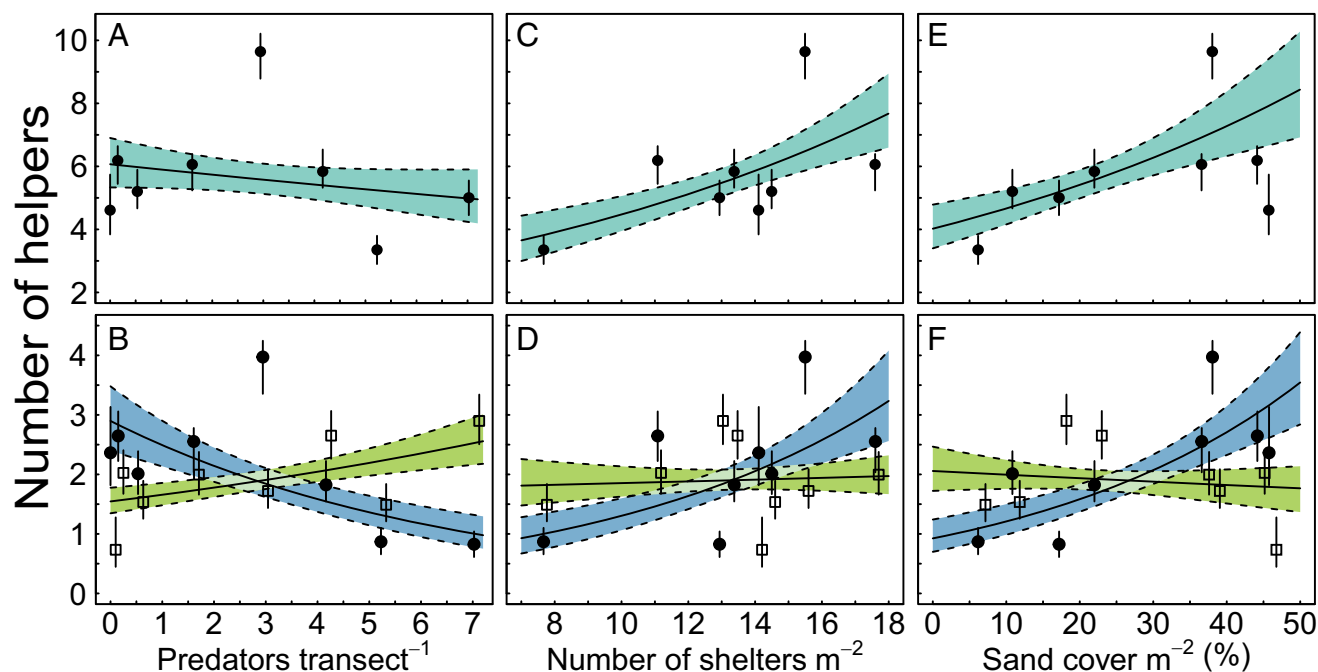
The cooperatively breeding cichlid fish *Neolamprologus pulcher* is a highly suited model system to unveil the role of predation risk as ecological constraint, as this species suffers from high predation (26), but usually not from a shortage of breeding sites (29). *N. pulcher* breeds colonially in sandy to rocky patches along the sublittoral zone (2- to 45-m depth) of Lake Tanganyika. Individual groups consist of a dominant breeding pair and up to 30 subordinates (25, 26, 30). Groups are frequently attacked by predatory fish (26), which significantly affects the survival probability of group members, especially small subordinates and fish devoid of protection through large conspecifics (31). Hence, membership in a group is a precondition for survival. Within groups, subordinates have to pay by helping in brood care, territory maintenance (i.e., removing sand and debris from underneath rocks), and defense to compensate for the costs they impose on dominant breeders (32–35), to which they are often unrelated (36). The lack of relatedness between larger subordinates and dominants reduces the opportunity for selective benefits of assisting kin, which differs sharply from the situation proposed for many other cooperative breeders (cf. 8, 37, 38). This finding suggests that other mechanisms are in place to explain helping behavior by larger subordinates (33, 39).

We investigated the effects of predation on the social organization of *N. pulcher*, using natural variation in predation risk and ecological factors shaping mortality, group composition, and behavioral decisions among eight distinct populations in Lake Tanganyika. Specifically, we focused our attention on shelter

availability and sand cover as ecological factors. Shelter availability has been shown to affect group size in this species (26), but not all group members may be equally dependent on access to shelters for their survival. In addition, territory maintenance has been shown to be one of the most costly activities in terms of time and energy expenditure (40, 41), and the extent to which helpers engage in these behaviors is likely dependent on the presence of sand in their territories.

## Results

**Between-Population Comparisons.** Habitat characteristics varied substantially between different populations (Fig. 1). The total number of helpers was not associated with predation risk (mean  $\pm$  SE = 0.026  $\pm$  0.020,  $P = 0.19$ ). However, predation risk showed an inverse relationship with small and large helpers: the number of large helpers increased with higher levels of predation (mean  $\pm$  SE = 0.093  $\pm$  0.021,  $P < 0.001$ ), whereas the number of small helpers decreased (mean  $\pm$  SE =  $-0.07 \pm 0.031$ ,  $P = 0.019$ ) (Fig. 1 *A* and *B*). The total number of helpers increased with rising numbers of shelters (mean  $\pm$  SE = 0.052  $\pm$  0.016,  $P = 0.001$ ), which was mostly because of the relationship between shelter availability and the number of small helpers. The number of small helpers increased significantly with a rising number of shelters (mean  $\pm$  SE = 0.063  $\pm$  0.024,  $P = 0.008$ ), and this relationship was more than twice as strong as for large helpers, where it was not significant (mean  $\pm$  SE = 0.025  $\pm$  0.017,  $P = 0.132$ ) (Fig. 1 *C* and *D*). Sand cover was positively correlated to total helper number (mean  $\pm$  SE = 0.011  $\pm$  0.004,  $P = 0.003$ ), again mainly because of the relationship between sand cover and the number of small helpers (mean  $\pm$  SE = 0.015  $\pm$  0.005,  $P = 0.004$ ), while there was no significant correlation with the number of large helpers (mean  $\pm$  SE = 0.004  $\pm$  0.004,  $P = 0.293$ ) (Fig. 1 *E* and *F*). Results of the relationship between these ecological variables and the number of medium-sized helpers are presented in Fig. S1 and Table S1.



**Fig. 1.** The relationship between predation risk (*A* and *B*), the number of shelters (*C* and *D*), and sand cover (*E* and *F*) with total number of helpers (*Top*) and group composition (*Bottom*) in different populations of *N. pulcher*. Population means and bootstrapped 95% confidence intervals are given for total helper number (filled circles in *A*, *C*, and *E*), small helpers (filled circles in *B*, *D*, and *F*), and large helpers (open squares in *B*, *D*, and *F*). Data points are slightly offset horizontally to avoid overlapping confidence intervals. Solid regression lines represent the model predicted values with bootstrapped predicted 95% confidence intervals for total helper numbers (teal), small helpers (blue), and large helpers (green).

**Within-Population Comparisons.** We used a subset of the data—all territories located within the habitat transects—to test whether these effects were also present within populations. We found a correlation between the number of shelters and the number of small helpers similar to that of the between-population comparison (mean  $\pm$  SE =  $0.040 \pm 0.021$ ,  $P = 0.049$ ) (Fig. 2A). However, within populations we found no significant correlation between sand cover and small helper numbers (mean  $\pm$  SE =  $0.006 \pm 0.005$ ,  $P = 0.255$ ). The number of large helpers was not correlated with the number of shelters or sand cover, but similar to the between-population data, both relationships were significantly greater for small helpers than for large helpers (number of shelters: number of small helpers vs. number of large helpers: mean  $\pm$  SE =  $-0.070 \pm 0.023$ ,  $P = 0.002$ ; sand cover: number of small helpers vs. number of large helpers: mean  $\pm$  SE =  $-0.022 \pm 0.005$ ,  $P < 0.001$ ).

Territories had fewer small helpers at lower densities (i.e., when neighbors were further away; mean  $\pm$  SE =  $-0.007 \pm 0.002$ ,  $P < 0.001$ ), and this effect was stronger under high predation risk (nearest neighbor distance  $\times$  predation risk: mean  $\pm$  SE =  $-0.014 \pm 0.005$ ,  $P = 0.003$ ) (Fig. 3). There was no significant correlation between the number of large and small helpers within groups (mean  $\pm$  SE =  $0.052 \pm 0.032$ ,  $P = 0.11$ ), and the number of large helpers did not depend on the distance to the nearest neighbor (mean  $\pm$  SE =  $-0.001 \pm 0.001$ ,  $P = 0.413$ ).

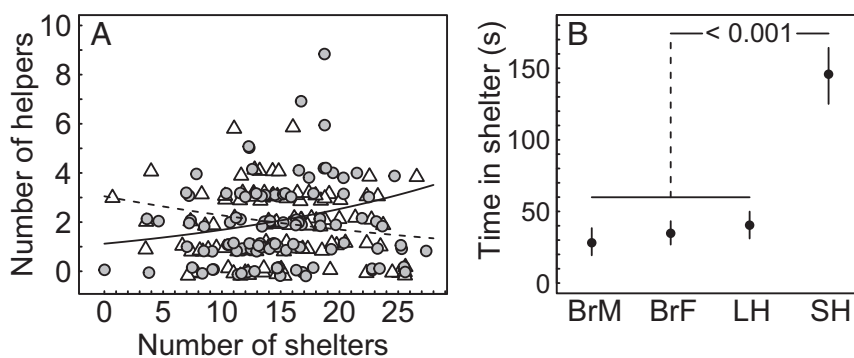
**Behaviors.** At higher densities, individuals showed fewer aggressive behaviors against predators (mean  $\pm$  SE =  $0.014 \pm 0.005$ ,  $P = 0.008$ ) (Fig. 4A), suggesting group members benefit from having nearby neighbors. In contrast, groups with more small helpers showed increased per capita predator defense rates (mean  $\pm$  SE =  $0.116 \pm 0.051$ ,  $P = 0.026$ ), whereas there was no effect of the number of large group members on per capita defense (mean  $\pm$  SE =  $0.174 \pm 0.127$ ,  $P = 0.171$ ), even though large helpers attack predators frequently (Fig. 4B).

Shelter maintenance behavior increased in populations with higher average sand cover (mean  $\pm$  SE =  $0.071 \pm 0.020$ ,  $P < 0.001$ ), and this effect was similar for all individuals (sand cover  $\times$  individual class:  $df = 3$ ,  $\chi^2 = 3.479$ ,  $P = 0.323$ ). Individuals lowered their shelter maintenance behavior with increasing predation risk, and small helpers decreased shelter maintenance more strongly than large helpers (slope small helpers vs. large helpers: mean  $\pm$  SE =  $0.301 \pm 0.114$ ,  $P = 0.008$ ). Predation risk was positively correlated with the time spent in shelters (mean  $\pm$  SE =  $3.384 \pm 1.689$ ,  $P = 0.046$ ), and this effect did not diverge between individuals of different sizes (predation risk  $\times$  individual class:  $df = 4$ ,  $\chi^2 = 6.040$ ,  $P = 0.196$ ). However, small helpers in

general spent significantly more time hiding in shelters than did other group members (mean  $\pm$  SE =  $116.791 \pm 8.839$ ,  $P < 0.001$ ) (Fig. 2B and Table S2) and also showed the greatest effort in the maintenance of these shelters (Table S3).

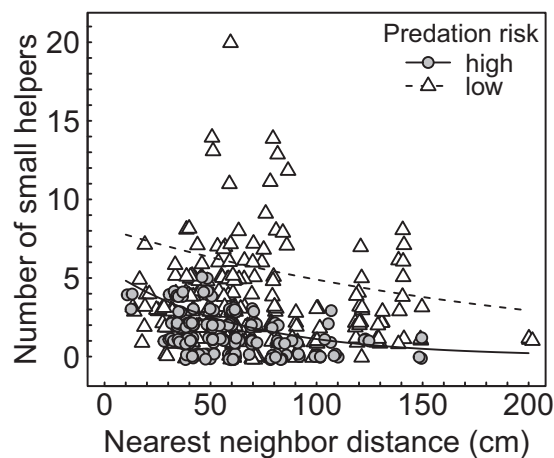
## Discussion

Habitat saturation and kin selection have been proposed as the primary explanations for the evolution and maintenance of the social complexity characteristic of cooperative breeders. Our results highlight that predation risk plays an important role in shaping the social organization and behavior of a cooperatively breeding fish, where habitat saturation and kin-selected benefits are arguably of negligible importance. Furthermore, the influence of predation risk apparently interacts with other important ecological factors. Consistent with our predictions, the social organization relates to the substantial variation between populations in predation risk and habitat characteristics. Predation risk poses a threat especially for small group members, which seem to benefit from enhanced access to shelters and from having close neighbors (Figs. 2A, 3, and 4A). Given that the number of small helpers within groups does not correlate with the number of large helpers, this finding suggests that small helpers may benefit more from enhanced security by the presence of close neighbors than from protection by large helpers in their own group (42). This pattern is consistent with our behavioral data: per capita predator defense increases with nearest neighbor distance, but not with the number of large group members (Fig. 4A and Table S4). This finding suggests that either predator dilution or benefits of shared defense are the primary contributors to the increased numbers of small helpers. A recent study on *N. pulcher* indeed revealed that individuals show reduced antipredator defense in response to the presence of close neighbors (43). Additionally, experimental data showed that a greater number of large group members increases survival in the group, except for small helpers (31). Another positive effect of close neighbors might be improved predator detection, enabling small helpers to take refuge from incoming predators in time. Increased predator vigilance is a major benefit of living in dense aggregations and colonies, especially when predators cannot be fended off by mobbing (2, 3). The importance of access to shelters for small helpers is illustrated further by the substantial time and energy expenditure that small helpers invest in creating and maintaining these shelters (Table S3), and by the positive relationship between shelter availability and the number of small helpers (Fig. 2A). Shelter maintenance has been shown to be the most energetically costly behavior in *N. pulcher*, raising standard metabolic rate sixfold (41), which strongly affects the helpers' behavioral energy budget (40). In addition, a field



**Fig. 2.** (A) Correlation between the number of small (shaded circles, solid line) and large (open triangles, dashed line) *N. pulcher* helpers with the availability of shelters. Data points are slightly offset to provide information on data density, and regression lines are drawn of mean predicted values based on mixed models accounting for between-population variance and the nonindependence of observations within territories. (B) Time spent in shelter for different individual classes of *N. pulcher* during 7-min observation periods. BrF, breeding female; BrM, breeding male; LH, large helper; SH, small helper. Error bars indicate 95% confidence intervals.





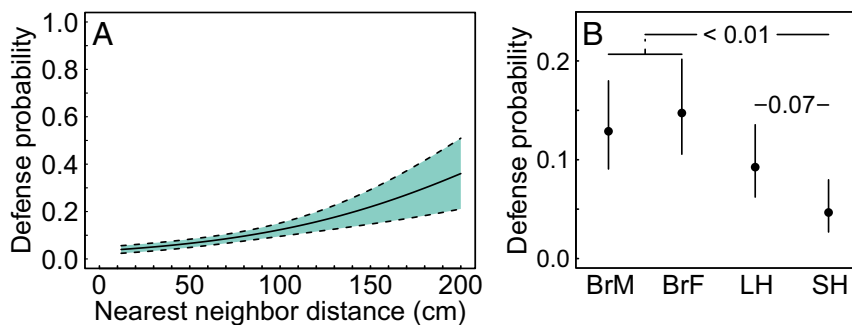
**Fig. 3.** Relationship between the number of small helpers in *N. pulcher* groups and the distance to the nearest neighboring group. The original data points are slightly offset to provide information on data density. Conditional regression lines are plotted for high (>median) and low (<median) predation risk based on mixed model mean predicted values accounting for the nonindependence of measurements within the same territories and colonies.

experiment revealed that group size depends on the number of shelters in the territory (26).

Delayed dispersal is regarded as an important first step in the evolution of cooperative breeding, and advanced sociality (44; but see refs. 45 and 46 for alternative pathways to group formation), and our results suggest that predation can be an important ecological factor selecting for this trait. Predation risk can affect individuals both during and after dispersal, as it also influences the reproductive potential of individuals that have obtained dominance in a new group. Subordinate *N. pulcher* have been shown to delay dispersal when the risk of predation is increased (31), and group members prefer to disperse to territories in the center of a colony (29), apparently to reduce the risk of predation by improved antipredator defense and vigilance. This may both increase survival of small helpers (Fig. 3) and decrease workload of group members in general, because of the combined antipredator defense of neighbors (43). One of the most pervasive results of this study is the obvious importance of access to shelters, especially for the survival probability of small individuals. The ability of groups to monopolize and provide access to shelters for small group members seems to be a crucial determinant of their survival and hence, of the reproductive success of breeders.

Our data show that per capita defense rates increase with the number of small helpers in the territory. Three alternative hypotheses can explain this observation. (i) Group members may be more aggressive toward potential predators when there are more juveniles present that are in need of protection. Active defense of helpers in need of protection by dominant group members has been shown experimentally in this system (30). (ii) Predators may preferentially target territories with a large number of small helpers, and hence they need to be repelled more often. The main predators of this species occur at higher densities inside of *N. pulcher* colonies than in adjacent areas (29), and it is conceivable that within colonies these predators focus on small group members because they are easier prey. Size-dependent choice of prey by piscivore predators has been observed in other species, and optimal foraging theory explains this as resulting from selection on the highest yield per time spent foraging (47). In addition, selection of small prey may involve a lower injury risk to predators. (iii) A large number of small helpers present in a group may increase conspicuousness to predators. The relationship between group size, conspicuousness, and predation risk has been well documented in numerous species (e.g., ref. 48). In accordance with this hypothesis, small subordinates in our study show reduced maintenance behaviors when faced with high predation risk (Table S3), which likely reduces conspicuousness. Similarly, in *Perisoreus* jays (*Perisoreus* spp.), subordinates seem to show helping behavior primarily under low risk of nest predation, which might reflect the necessity to conceal the nest location if predators of young are abundant (49). We should point out that these three hypotheses are not mutually exclusive. They may in fact jointly explain the observed correlation between the number of small group members and individual defense effort.

In addition to these apparent direct effects of predators on group structure and behavior, between populations the number of small helpers per group increased significantly with sand cover. Two mutually nonexclusive explanations could account for this pattern. First, shelter maintenance by digging is the most energetically costly behavior in this species (40), which is likely to be partly responsible for the stunted growth of helpers (30, 40). This might result in group compositions being skewed toward small individuals, because investment in maintenance declines with increasing body size (Table S3). Second, sand allows for ecological niche construction by digging out shelters, and thereby manipulating the environment (50). Although rocky habitat may provide shelters that are more easily accessible, requiring a smaller initial investment and potentially lower maintenance costs, their number and size cannot be modified. Hence, group composition in *N. pulcher* may partly depend on the environmental potential for niche construction,



**Fig. 4.** Per capita probability of predator defense of *N. pulcher* in relation to nearest neighbor distance (A), and class of group members (B). BrF, breeding female; BrM, breeding male; LH, large helper; SH, small helper. The solid and dashed lines in A indicate the predicted values and bootstrapped 95% confidence intervals, respectively. In B, means and SEs are shown. Model parameter estimates for the significance values are given in Table S4.

which might be an important evolutionary driver of social organization both in *N. pulcher* and in general.

The effects of predation risk on the transition to complex social organization have been underexplored. Our study demonstrates significant effects and interactions between predation risk and other ecological factors affecting survival, social structure, and behavior of a cooperatively breeding vertebrate in the wild. An important strength of this study is that most of our studied populations were in close vicinity to each other, therefore geographical distance and correlated patterns of gene flow cannot explain the results. In fact, the two populations that shared the smallest between-population distance showed the highest ecological differentiation in almost every aspect. The significance of the results of this study extends far beyond the evolutionary ecology of cooperative breeding. Predation risk has been invoked as a prime ecological driver in the evolution of group living of primates and early hominids, mostly by relating predation risk to group size (51, 52). However, our study shows that predation may affect group composition and behavior more strongly than group size, especially when interactions between predation risk and other ecological factors are considered. Hence, this study highlights the importance of predation risk as a major factor, selecting not only for the formation of groups but for complex social organization.

## Materials and Methods

**Sampling Sites, Predation Risk, and Ecological Factors.** We collected data on eight different populations of *N. pulcher* between September and December 2012 and 2013 by SCUBA-diving at the southern end of Lake Tanganyika. Populations were on average 1,796 m apart (range = 150–22,450 m), with seven populations all being within 9 km of each other and one population located about 20 km away from the rest.

We estimated predation risk in each population along four transects of  $10 \times 1 \text{ m}^2$  by counting the number of fish predators (*Lepidolamprologus elongatus*, *Lepidolamprologus attenuatus*, and *Lamprologus lemairii*). We repeated these scans between 6 and 10 times per population on different days to capture the variation in fish activity. For each population we estimated predation risk on adult *N. pulcher* by calculating the mean number of large (>10 cm) *L. elongatus* and *L. attenuatus* per transect (31). *L. elongatus* and *L. attenuatus* are the most common predators of *N. pulcher* in our study area (26, 29, 31) and they were also the two most abundant species in the surveyed populations. These are highly mobile predators, usually observed in small groups moving through our populations at 20–30 cm above ground looking for prey, which in the case of *N. pulcher* consists mainly of smaller fish or fish devoid of protection by a group (30, 31).

We measured the number of shelters and the percentage of sand cover per square meter (hereafter “sand cover”) for each population by surveying four transects of  $10 \times 1 \text{ m}^2$  of bottom substrate, starting from the center of a colony and moving outwards in four directions at  $90^\circ$  angles. We also determined how many of these shelters were used by *N. pulcher* or other species, whether the respective square meter contained an *N. pulcher* territory and if so, the proportion of area covered by *N. pulcher* territories. To check for within-population correlations between group and habitat characteristics, we recorded the group compositions according to different size classes for all territories located within these transects, described in detail below.

**Group Compositions, Group Sizes, and Densities.** For between-population comparisons, we used data from 20 territories sampled at random from each population. We searched for *N. pulcher* territories in each of the eight populations until we were confident that all territories had been detected. The boundaries of *N. pulcher* colonies were established where no other territories were found within 5 m of the outermost territories of the colony, except for two very large populations where, because of practical considerations, artificial boundaries were established despite other territories being close by. All territories were individually marked with small numbered stones (~5 cm in diameter). In each population we determined the group composition for each randomly selected territory. We estimated the standard length (SL; from tip of the snout to the posterior end of the last vertebrae) of individuals, and assigned them to different size classes: fry (<0.5 cm), nonhelpers (0.5–1.5 cm), small helpers (1.6–2.5 cm), medium helpers (2.6–3.5 cm), large helpers (>3.5 cm) following Heg et al. (31). Our analyses focus mainly on the differences between small and large helpers, because these represent nonoverlapping size classes and previous studies have shown clear

differences in behavior and mortality risk as a result of predation (31, 53). For example, small helpers typically do not disperse, whereas large helpers do disperse if conditions allow (54, 55). In addition, predation risk differs markedly between small and large helpers also with regard to group size effects (31). Medium-sized helpers, in contrast, form a transitional state that is intermediate in both life history decisions and behavior, and their predation risk is also intermediary (31). Therefore, there are no clear hypotheses regarding the variation of their numbers according to ecological factors. However, we provide information about these relationships in Fig. S1. We also recorded the presence or absence of dominant breeding females and males. Dominants can easily be distinguished from subordinates based on size and behavior. Because not all subordinates in a group were always visible (e.g., as a result of time spent hiding or feeding in the water column) we estimated group composition repeatedly for each territory (median = 3 times, range = 1–4). For one population, only a single measure of group composition per territory could be obtained. From these group compositions we also calculated total group size (i.e., the total number of helpers). For each focal territory, we measured the distance to the nearest neighboring territory from the center of each territory to the nearest 5 cm and counted the total number of territories present within a 2-m radius, as a measure of territory density.

**Behavioral Observations.** In each focal group we recorded the behavior of both dominant breeders and of one haphazardly selected individual from each subordinate size class. All behaviors were recorded continuously for 7 min using a handheld computer (Psion Teklogix Workabout Pro-7525) in a waterproof plastic bag, running Noldus Pocket Observer (v3.0). Recorded behaviors included aggression against predators, group members, and other conspecifics, which was either overt (chasing, ramming, biting, mouth fighting, or other forms of elevated aggression) or restrained (spreading of fins or opercula, head down display, s-bend swimming, or fast approach); submissive behaviors toward dominants and other group members (tail quiver, hook swimming, and bumping); and maintenance behaviors (removal of sand and debris from the territory) (9, 30). We also observed the spacing behavior of focal individuals continuously during the observation and recorded whether they were inside their home territory ( $\pm 30$ -cm semispherical dome around breeding shelter) (9), visiting another territory, outside of any territory, or in a shelter. In total, we collected 77 h of behavioral data of 660 individual fish in 154 different territories.

**Statistical Analyses.** We analyzed between-population effects on the total number of subordinates and the number of large and small subordinates by fitting these as separate response variables in a generalized linear mixed model (GLMM) assuming a Poisson error distribution. To see how the number of small helpers related to territory density and the number of large helpers in the territory, we fitted a Poisson GLMM. Territory defense was analyzed as a binary trait in a GLMM where we included individual class, the number of small and large helpers in the territory, nearest neighbor distance, and predation risk as predictor variables. To assess whether shelter maintenance was affected by sand cover and predation risk, and whether this relationship varied between different individuals, we fitted a Poisson GLMM with interactions between both sand cover and predation risk, and individual class and predation risk. We analyzed the time spent hiding in shelters by fitting a linear mixed model with predation risk, nearest neighbor distance, individual class, and the interaction between predation risk and individual class as predictors. For all models, we fitted varying intercepts for *Territory ID*, and where necessary *Population ID*, to account for the nonindependence of repeated measurements within these groups. We used an information theoretic model selection approach to find the most parsimonious model. Variables were removed from the model if dropping that variable resulted in a model with a minimum difference of two Akaike Information Criterion (AIC<sub>c</sub>) values (56). We calculated conditional  $R^2$  based on Nakagawa and Schielzeth (57) as an estimator of the explained variance. Parameter significance was inferred based on likelihood ratio tests of deviances assuming a  $\chi^2$ -distribution. All models were inspected for violations of model assumptions, such as overdispersion, deviations from normality, and heteroscedasticity. All data were analyzed in R v3.1.2 (58) using the packages “lme4” (59), “nlme” (60), and “AICcmodavg” (61) for parameter inference and model selection.

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