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Author for correspondence:
Markus Zöttl
e-mail: mz338@cam.ac.uk

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Group size adjustment to ecological demand in a cooperative breeder

Markus Zöttl[1,2], Joachim G. Frommen[1] and Michael Taborsky[1]

[1]Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, 3032 Hinterkappelen, Switzerland
[2]Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

Environmental factors can determine which group size will maximize the fitness of group members. This is particularly important in cooperative breeders, where group members often serve different purposes. Experimental studies are yet lacking to check whether ecologically mediated need for help will change the propensity of dominant group members to accept immigrants. Here, we manipulated the perceived risk of predation for dominant breeders of the cooperatively breeding cichlid fish *Neolamprologus pulcher* to test their response to unrelated and previously unknown immigrants. Potential immigrants were more readily accepted if groups were exposed to fish predators or egg predators than to herbivorous fish or control situations lacking predation risk. Our data are consistent with both risk dilution and helping effects. Egg predators were presented before spawning, which might suggest that the fish adjust acceptance rates also to a potential future threat. Dominant group members of *N. pulcher* apparently consider both present and future need of help based on ecological demand. This suggests that acceptance of immigrants and, more generally, tolerance of group members on demand could be a widespread response to ecological conditions in cooperatively breeding animals.

1. Introduction

In cooperatively breeding animals subordinates help raise offspring produced by dominant breeders [1–3]. Subordinates contribute to many different tasks such as cooperative hunting and foraging [4–6], territory defence and maintenance [7–9], sentinel behaviour [10,11], and direct brood care such as provisioning [12–14], guarding of young [15–18], and cleaning eggs and larvae [19,20]. This can increase the fitness of the breeding individuals, for instance, by raising offspring production [2,3,19,21–24]. The mere presence of subordinate group members can generate positive fitness effects on other group members as well, for instance, by dilution effects, predator confusion and deterrence [25–27]. The different fitness benefits accrued to dominant and other group members by subordinate helpers are not mutually exclusive.

Subordinates can also impose costs to breeding individuals, for instance by participating in reproduction and competing for resources, which can reduce reproduction or growth of breeders [18,28–30]. The cost–benefit ratio of the presence of subordinates in the group depends strongly on the environmental conditions [19,31,32]. For example, if the subordinates' contribution to territory defence provides a benefit to breeders, subordinate group members are more beneficial to have under high risk of predation or competition for territories. Dominant individuals, which often have control over group size, can strategically adjust group size to changes in the cost–benefit ratio by evicting subordinates from the group if they become too costly [31,33,34]. For example, in several cooperatively breeding mongooses, dominant females often expel pregnant subordinate females as they impose high costs particularly to the dominant female [28,33,35].

While the regulation of group size by dominant breeders through eviction of subordinates has been commonly observed in different cooperatively breeding species [31,33,36], the opposite possibility of extending cooperative groups by allowing immigration into the group if required by environmental conditions has been scarcely documented. Evidence that dominant breeders accept additional helpers more readily with increasing benefits of help exists from pied kingfishers (*Ceryle rudis*), where experimental clutch enlargement increased helper presence [37]. An opposite regulatory effect was observed in the clown anemonefish (*Amphiprion percula*), where dominant group members prevent immigration when the group is saturated [36]. Indirect evidence for group size adjustment to demand exists from baywings (*Agelaioides badius*), where more helpers were present when nests were parasitized by cowbirds (*Molothrus* spec.), which resulted in a higher begging intensity in the nest [38]. In the cooperatively breeding cichlid, *N. pulcher*, evicted offspring can be reaccepted when competition for the territory is experimentally increased, suggesting that breeders in this species are able to estimate their need for help [31]. Hitherto it is unknown, however, whether cooperative breeders respond to variation of predation risk by adjusting their acceptance of alien immigrants into the group. An effect is expected given that one major benefit of additional group members results from their contribution to territory defence [7,23,31] and dilution and predator confusion effects [25,26,39]. *Neolamprologus pulcher* provides excellent opportunities to investigate experimentally the response of dominant breeding individuals to changes in their cost–benefit ratio that might be associated with the presence of additional group members. It breeds in cooperative groups of up to about 30 individuals [7,39,40]. Smaller group members are queueing for breeding positions in sex-specific hierarchies or for opportunities to disperse into neighbouring territories [41–43]. Subordinates of both sexes and various sizes participate in brood care by cleaning and fanning the eggs [19,44], in territory defence against predators, space competitors and conspecific intruders [7,19,31,45], as well as in territory maintenance ([19], for review see [46]). Thereby, helpers specialize on different tasks depending on their body size [47]. Helper presence enhances survival of fry in the territory [23] and allows the breeder female to reduce energy investment and to produce larger clutches [19,48]. Nevertheless, helpers also impose costs by reducing growth rate of female breeders [30] and sometimes participating in reproduction, which can lead to eviction of costly subordinates from the territory [18,29,44].

Here, we manipulated perceived risk of predation for groups of *N. pulcher* to test whether this affects acceptance of an additional, unknown and unrelated subordinate in their territory. We exposed experimental groups either to predators of juvenile and adult fish (*Lepidiolamprologus elongatus*) or eggs and larvae (*Telmatochromis vitattus*). We predicted that the propensity to accept further helpers rises with increasing predation pressure. Specifically, we made two diverging predictions contingent on the type of benefit breeders might attain from additional group members; (i) if breeders mainly benefit from ‘safety-in-numbers’ effects (dilution and predator confusion), enhanced immigrant acceptance should be confined to increased risk of predation resulting from large predators that prey on fish, and it should be largely independent of immigrant size; (ii) if breeders mainly benefit from the contributions of subordinates to territory defence, they should generally accept immigrants when predation pressure is increased, also when this includes predators of eggs and larvae. Egg predators do not prey on fish of breeder size and accordingly, breeders would not benefit from accepting immigrants if the major benefit derived from additional group members is risk dilution. Thus, immigrant acceptance in the egg predator treatment should be raised only if their active contribution to territory defence yields fitness benefits to the breeders. In control trials, *N. pulcher* groups were exposed either to no intruders at all or to strictly herbivorous cichlids that would not cause benefits from group augmentation neither by risk dilution nor from enhanced territory defence.

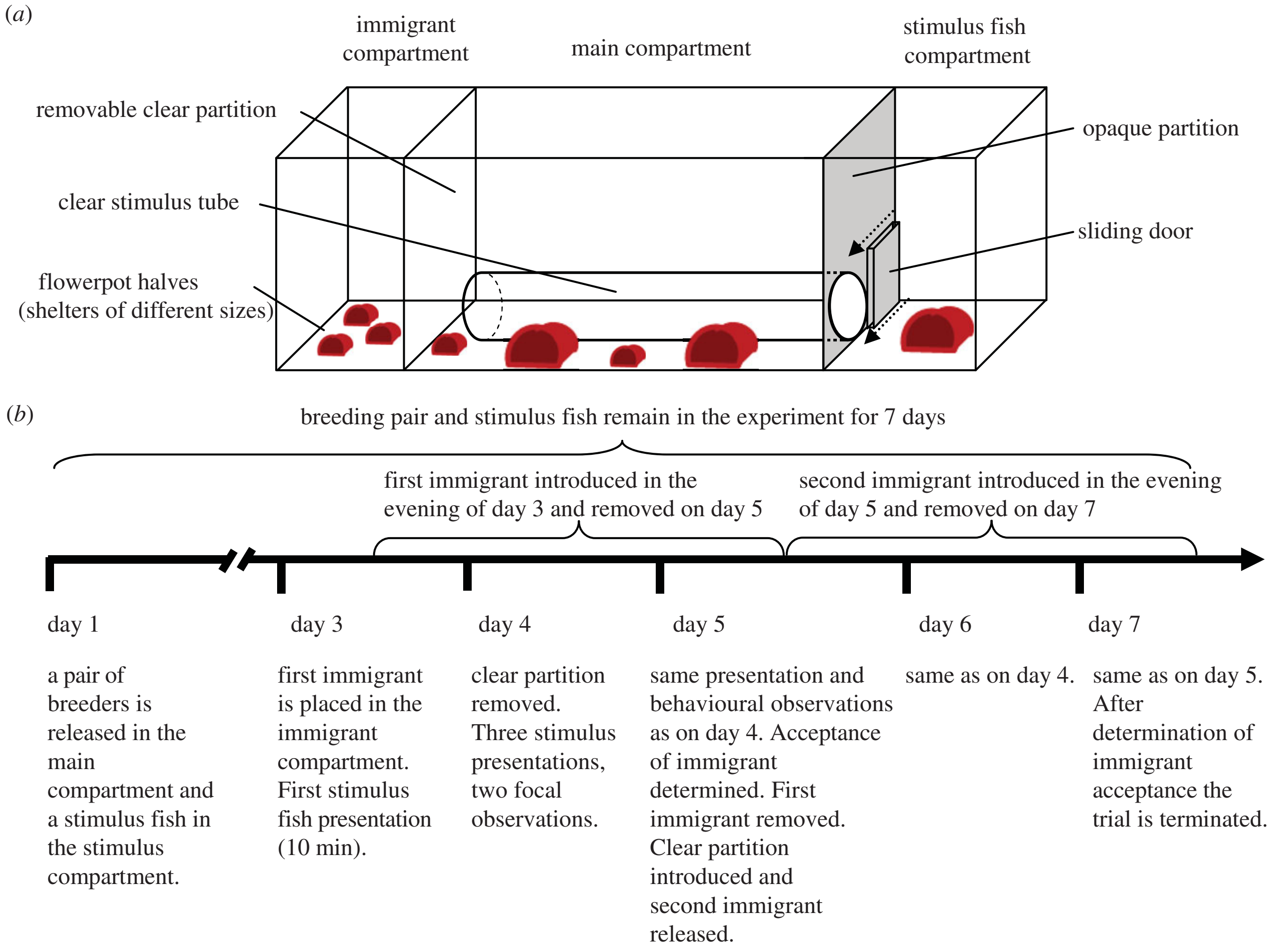
2. Material and methods

(a) Fish used in this study

All fish used in this study are endemic to Lake Tanganyika, east Africa, where they live in sympatry along the lake shore [49–51]. *Neolamprologus pulcher* used in this experiment were descendants from fish caught in the wild in the years 1999, 2006 and 2009, at Kasakalawe point and Mbita Island. Both locations are at the southern tip of lake Tanganyika, close to Mpulungu. *Neolamprologus pulcher* is distributed all along the shore of Lake Tanganyika at a depth of 3–45 m [7,52]. *Neolamprologus pulcher* have been kept in separated tanks in non-reproductive aggregations. In the ‘fish predator treatment’ we used the piscivorous cichlid *L. elongatus* as stimulus fish. *Lepidiolamprologus elongatus* preys on all size classes of *N. pulcher* except eggs and is probably its most important predator [7,19,32,40]. In the ‘egg predator treatment’ we used *Telmatochromis vittatus*, a small shell-brooding cichlid common in *N. pulcher* colonies [47]. Their slender body shape allows them to enter breeding cavities of *N. pulcher*, and they are regarded to be one of their most important predators of eggs and larvae [47,53], employing sneaky intrusions into the territories of substrate brooding cichlids [54]. Note that this experiment was conducted before spawning, i.e. *N. pulcher* pairs had no clutches to defend during the whole experimental period. However, egg predators become a threat right after spawning takes place, i.e. in the near future. In the ‘herbivore treatment’, we used *Ophthalmotilapia ventralis*, a sympatric algae eating cichlid posing no threat to eggs, young or adults of *N. pulcher*. *Ophthalmotilapia ventralis* is common at the southern tip of Lake Tanganyika, occuring at depths between 2 and 15 m [50,51,55]. Ecological surveys documented sympatry of *N. pulcher* and *O. ventralis* close to Mpulungu [49,51], and *O. ventralis* has been observed to occasionally invade territories of substrate brooding cichlids such as *N. pulcher*, where they are actively chased [49]. Finally, in the ‘control without fish’ we did not use any stimulus fish but performed all manipulations in the aquarium exactly as in the three other treatments. Note that the three stimulus fish types differed in size with the fish predators being largest (mean body size = 129 mm, range = 94–145 mm), herbivores having intermediate body size (mean body size = 59 mm, range = 53 mm–69 cm) and the egg predators being smallest (mean body size = 46 mm, range = 40–58 mm).

(b) Experimental set-up

The experiment was conducted in 200l tanks at the Ethologische Station Hasli, Institute of Ecology and Evolution, University of Bern, Switzerland, between February and July 2011 under the license 16/09 of the Veterinäramt Bern. Experimental 200 l tanks (100 × 40 × 50 cm) were subdivided into three compartments: a main compartment (60 cm length) inhabited by a pair of breeders, an immigrant compartment (15 cm length) and a stimulus compartment (25 cm length) containing the respective stimulus fish (figure 1*a*).The main compartment was separated from the helper compartment by a clear partition and contained



day 1: a pair of breeders is released in the main compartment and a stimulus fish in the stimulus compartment.

day 3: first immigrant is placed in the immigrant compartment. First stimulus fish presentation (10 min).

day 4: clear partition removed. Three stimulus presentations, two focal observations.

day 5: same presentation and behavioural observations as on day 4. Acceptance of immigrant determined. First immigrant removed. Clear partition introduced and second immigrant released.

day 6: same as on day 4.

day 7: same as on day 5. After determination of immigrant acceptance the trial is terminated.

Figure 1. (*a*) The experimental tank with its three compartments. (*b*) Time schedule of the experimental procedures and behavioural observations. (Online version in colour.)

four flower pots halves as shelters. The stimulus compartment was separated by an opaque partition to prevent visual contact between stimulus fish and *N. pulcher*. In the middle of the partition was a sliding door connecting the stimulus compartment to a clear stimulus tube (50 cm length and 14.5 cm diameter), covered by a net on one end. This stimulus tube reached into the centre of the main compartment to allow the stimulus fish to swim into the territory while preventing direct physical contact between stimulus fish and *N. pulcher*. The immigrant compartment contained three small flower pot halves and a semi-opaque plastic bottle suspended next to the surface as an additional hide. The stimulus compartment contained a shelter to reduce stress of the stimulus fish.

(c) The experimental procedure

Pairs were established by putting a male and female *N. pulcher* together in the main compartment on day 1 of the experiment (figure 1*b*). On the same day, the respective stimulus fish were placed in the stimulus fish compartment. At the start of the experiment, the body size of all fish were determined. We measured standard length, which is the maximal extension of the body from the tip of the mouth to the caudal peducle (later referred to as 'body size'). To resemble natural conditions [7,40], the male breeder was the largest individual in each group of each replicate (mean body size = 66 mm, range: 55–77 mm); female breeders were slightly smaller than males (mean body size = 59 mm, range: 51–68 mm; mean body size difference between male and female breeders = 7.0 mm, range: 1–16 mm) and immigrants were the smallest individuals (mean body size = 36 mm, range: 27–49 mm; mean body size difference to female breeder = 20 mm, range: 6–34 mm; mean body size difference to male breeder = 27 mm, range: 14–39 mm). The potential immigrants included individuals of both sexes which were housed with similar sized fish in mixed-sex aggregations. The size differences between male, female and the potential immigrant were not significantly different between the four treatments ($p > 0.6$).

On day 3, we checked whether the male and female breeder had established a pair bond, which was determined when both breeders entered the same caves and by the lack of continuing aggressive interactions. In the evening of day 3, the first immigrant was placed in the immigrant compartment and the initial stimulus fish presentation was conducted. A stimulus presentation was started by opening the door between the stimulus compartment and the transparent tube in the main compartment (figure 1*a*). Subsequently, the stimulus fish was gently guided into the tube using hand nets where it was visible to the breeding pair and the immigrant. The initial stimulus presentation (days 3) lasted 10 min. On days 4–7, stimulus presentations of 5 min each were performed three times a day (figure 1*b*). After the presentation, the stimulus fish was guided back into the predator compartment and the sliding door was closed. During the presentation, the stimulus fish was visible for all experimental fish, but no physical contact between predator and the experimental individuals was possible at any time. In the morning of day 4, we removed the partition between the potential immigrant and the breeders. Typically, the fish started interacting as soon as the partition had been removed. Previous studies revealed that fish below 50 mm SL usually try to get accepted in a group even if suitable habitat is available and predators are absent [31,56], while the breeders display variable amounts of aggression against them.

In all replicates, the breeders enlarged their territory to also include the immigrant compartment and all flower pot halves as soon as the partition was removed, and subsequently either accepted the smaller individual as group member or expelled it from the territory. Evicted group members were attacked when approaching the bottom area and the shelters and thus usually stayed in the water column close to the surface, or hid in the suspended bottle. Each pair was tested twice with two immigrants of different sizes, one at a time and introduced in randomized size order. The first immigrant was put in the tank on day 3 and removed on day 5. Then the immigrant compartment was installed again by introducing the clear plastic sheet and the second immigrant was subsequently introduced on day 5. Starting in the morning of day 6, the second trial was conducted in the same way as the first trial, and it ended on day 7.

We carried out one observation block per day on days 4–7. An observation block consisted of three observations. First, we recorded the number of aggressive displays from the breeders towards the potential immigrant for 10 min. Then we conducted a stimulus fish presentation and counted the number of attacks against the presented stimulus fish by the male, the female, and the potential immigrant. Afterwards, we again recorded the behaviour of the breeders towards the immigrant for a further 10 min. We scored the immigrant as ‘accepted’ or as ‘evicted’, depending on their behaviour and interaction with the breeders. The eviction status was finally determined after the immigrant was allowed to have contact to the breeders for two days; i.e. on day 5 for the first immigrant and on day 7 for the second immigrant. Aggression of breeders against helpers is most intense during egg laying, when helpers suffer a much higher risk of being expelled from the group [31]. As it was not our aim to investigate the influence of the presence or absence of eggs on immigrant acceptance rate, four replicates out of 55 had to be removed because the pair produced a clutch during the experiment. Furthermore, one pair had to be excluded as they established no pair bond, leading to a final dataset of 50 breeding pairs and 100 immigrants. In one replicate, the last behavioural observation could not be conducted as the immigrant in the fish predator treatment accessed the predator compartment and was predated, reducing the sample size from $N = 100$ to 99 for behavioural analysis of aggression between breeders and immigrants. In this case, we used the last conducted measure of acceptance for the analysis. Aggression against the stimulus fish was analysed only for treatments involving stimulus fish (excluding the control without fish), and thus yield a sample size of $N = 75$ for breeders and $N = 38$ for accepted immigrants.

(d) Statistical analysis

Attack rates against the stimulus fish on days 4 and 5 (with the first immigrant) and on days 6 and 7 (with the second immigrant) were summarized, respectively, resulting in two values per pair and one value per immigrant. Similarly, the aggression rates of breeders against immigrants were calculated by summarizing the numbers of aggressive behaviours directed from the male and female breeder towards the immigrants during all four focal observations. This yielded two different aggression rates per pair member, one each against both potential immigrants.

All statistics were calculated using R v. 2.13.1 [57]. We used generalized linear mixed effect models of the package lme4 [58] with log link accounting for Poisson distributions (for attack and aggression rates) and probit link accounting for binomial distributions (for probability of acceptance). We included the pair identity as a random factor and added treatment as a fixed factor in all analyses. To model eviction probability, we included the size differences between breeders and immigrant as a covariate in the full model. When analysing aggression against immigrants from the pair, we additionally added the eviction status, sex of the breeder and their interaction as fixed factors. We calculated full models and reduced non-significant terms stepwise. The order in which the immigrants were exposed to the breeder (being the first immigrant on days 4 and 5 or the second immigrant on days 6 and 7) had no significant effect and was therefore omitted in the models displayed below. Data are deposited in the Dryad digital repository [59].

3. Results

(a) Acceptance of immigrants in groups

The probability of being accepted as a subordinate in the territory depended on the treatment. Immigrants in the fish predator and egg predator treatments experienced a higher probability of being accepted as group members compared with the two control treatments (figure 2, table 1*a*). The acceptance rate in the fish predator treatment did not differ significantly from the acceptance rate in the egg predator treatment. Furthermore, the two controls did not differ significantly from each other (figure 2, table 1*a*). Besides the treatment, the difference between female body size and immigrant body size influenced the probability of acceptance as a group member (figure 2, table 1*a*); immigrants with a large size difference to the breeder female were more readily accepted. The absolute body size and the difference in body size between male breeder and immigrant had no influence on the probability of acceptance (both $p > 0.1$).

(b) Territory defence

Accepted immigrants contributed most in territory defence against egg predators and showed very low contributions to territory defence against fish predators and herbivore intruders (figure 3; table 1*e*). Male breeders attacked fish predators and herbivore intruders significantly more often than egg predators, whereas female breeders attacked herbivore intruders significantly more often than fish or egg predators (figure 3, table 1*c*, *d*).

(c) Aggression against immigrants

Overall, immigrants that were finally evicted received more aggression than finally accepted ones (table 1*b*). Aggression rates against immigrants did not differ between breeder males and females. If immigrants were evicted, however, male breeders increased their aggression rate more than female breeders did (table 1*b*). Thus, despite the fact that the size difference between the immigrant and the female breeder determined acceptance (figure 1; table 1*a*), male breeders seemed to play an important role in territory defence against unwanted immigrants (table 1*b*).

4. Discussion

Our data show that the exposure of *N. pulcher* groups to predators of eggs, larvae, juveniles and adults raises the acceptance rate of previously unknown and unrelated individuals into their group. This is likely to be an adaptive response to enhanced predation pressure. In the case of fish-eating predators, breeders in larger groups might enjoy the advantage of common territory defence and increased dilution effects [39,60,61]. However, the contribution of the accepted

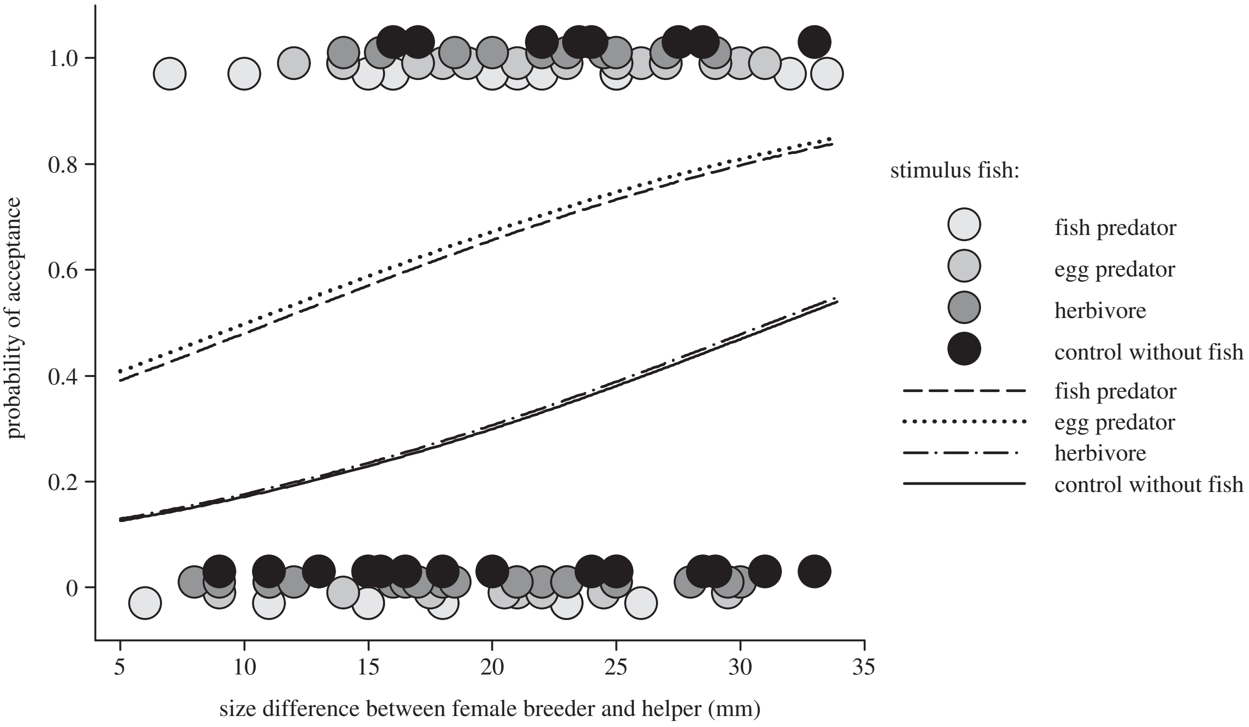


Figure 2. The probability of acceptance of an immigrant in four treatments in relation to difference in body size (in mm) between the dominant female and the immigrant (potential helper). The four lines indicate the predicted values from the fitted model (see table 1 for model details). Dots symbolize data points; $y = 1$ indicates acceptance, whereas $y = 0$ indicates eviction. Note that for better visibility the dots are slightly off-set along the y-axis.

subordinates to territory defence against fish predators was low and only marginally significant. This suggests that the main benefits breeders gain from accepting immigrants of this size in the fish predator treatment arise from risk dilution or predator confusion effects, which is consistent with correlative data from the field [34]. In contrast, when predation on eggs is concerned, such dilution effects cannot occur. Instead, breeders might benefit from an increase in defence against egg predators by the accepted immigrants, as helpers specialize in such defence also in the field [7,47]. Indeed accepted immigrants contributed to defence against egg predators more than against any other type of intruder. We suggest that these two mechanisms, joint predator defence and risk dilution, both yield substantial fitness benefits of additional group members to the dominant breeders. These benefits outweigh the costs that additional group members may cause to breeders, such as enhanced brood parasitism, cannibalism and growth reduction [18,19,30].

An alternative explanation to deliberately enhanced immigrant acceptance by breeders could be that immigrants were more eager to stay in the territory under high perceived predation pressure. However, our data suggest that increased immigrant acceptance was rather caused by a strategic decision of the breeders: first, immigrant acceptance was explained by lower aggression rates from breeders towards immigrants. Second, the probability of immigrant acceptance was observed to be high in the egg predator treatment, whereas, for an immigrant, only a fish predator enhances the immediate benefit of being accepted in a safe territory.

Egg predators were presented in this experiment at a time when the breeding pair had not yet spawned. This implies that at the time when the breeders decided about immigrant acceptance, the egg predators had no possibility to hamper *N. pulcher* reproduction. Nevertheless, the egg predator treatment raised immigrant acceptance to the same level as in the fish predator treatment. This suggests that breeders of this species might be able to anticipate a potential future threat and adjust their behaviour strategically to maximize fitness in the future rather than at the time of the decision to accept or repel an immigrant. This process seems to resemble future planning as shown in birds and apes [62,63], but further experiments are needed to unravel the mechanisms underlying this seemingly anticipatory behaviour and conclusively rule out alternative explanations.

Strategic adjustments of group size by immigration and eviction are particularly likely to be important in cooperative systems with task specialization, because individuals engage in divergent tasks that can be of different importance under certain ecological circumstances [47]. However, this argument holds only in social systems where direct benefits to helpers provide an important incentive to help. Cooperative breeders matching these criteria are found across many taxa including fish (size-dependent task specialization [7,47]; birds (age-dependent engagement of helpers in incubation and provisioning of nestlings) [2,64]; social mammals (age-dependent polyethism [65] or division of labour [66]); and social insects (division of labour [67,68]). Recent evidence suggests that direct fitness benefits might be more important than previously thought, even among primitively eusocial insects [69,70].

Previous studies in cooperatively breeding birds suggest that the acceptance of subordinate group members can be contingent upon provisioning demands of nestlings [37,38]. Furthermore, agonistic interactions with rivalling conspecifics can influence sociability [71,72] and cooperative propensity in humans [73] and other animals. In the cooperatively breeding green woodhoopoe (*Phoeniculus purpureus*), for instance, more affiliative behaviour is directed from breeders to subordinates when they move into zones of their territories where aggressive encounters with rival groups are more frequent [74].

Table 1. Statistical models for (*a*) the acceptance of subordinates ($N = 100$), (*b*) aggression against subordinates ($N = 99$), the attacks of (*c*) males ($N = 75$), (*d*) females ($N = 75$) and (*e*) accepted immigrants ($N = 38$) against predators. See §2 for explanation for diverging sample sizes.

	estimate ± s.e.	*z*-value	*p*-value
(*a*)			
empty control (intercept)	−2.43 ± 0.94	−2.60	<0.01
herbivore	0.03 ± 0.63	0.05	0.96
fish predator	1.58 ± 0.69	2.28	0.02
egg predator	1.66 ± 0.69	2.40	0.02
fish predator versus herbivore	−1.54 ± 0.64	2.41	0.02
fish predator versus egg predator	0.08 ± 0.69	0.11	0.91
egg predator versus herbivore	−1.62 ± 0.65	-2.51	0.01
difference SL female-immigrant	0.08 ± 0.04	2.16	0.03
(*b*)			
male breeder (intercept)	1.04 ± 0.19	5.58	<0.01
female breeder	−0.06 ± 0.10	−0.60	0.55
status (evicted)	0.72 ± 0.22	3.29	<0.01
sex*status (evicted)	−0.24 ± 0.12	−1.96	<0.05
(*c*)			
fish predator (intercept)	3.19 ± 0.47	6.86	<0.01
egg predator	−1.54 ± 0.67	−2.29	0.02
herbivore	0.42 ± 0.60	0.69	0.49
egg predator versus herbivore	1.95 ± 0.62	−3.16	<0.01
(*d*)			
fish predator (intercept)	1.50 ± 0.43	3.50	<0.01
egg predator	0.16 ± 0.60	0.26	0.79
herbivore	2.22 ± 0.55	4.06	<0.01
egg predator versus herbivore	2.06 ± 0.55	−3.78	<0.01
(*e*)			
fish predator (intercept)	−1.60 ± 0.85	−1.89	0.06
egg predator	4.26 ± 1.03	4.12	<0.01
herbivore	1.51 ± 1.12	1.34	0.18
egg predator versus herbivore	−2.75 ± 0.94	2.91	<0.01

In *N. pulcher*, increased competition by conspecifics and heterospecifics for the territory, which includes shelters, breeding substrate and food for young, has been shown to affect aggression from breeders towards subordinate group members and to facilitate reacceptance of previously evicted helpers [31]. This apparent effect of resource competition on group stability impinges on group size like the incorporation of alien conspecifics into the group as demonstrated in our study. However, divergent proximate and ultimate mechanisms underlie these different group size adjustments. In the experiments of Taborsky [31], familiar offspring of the pair that had been recently expelled were allowed access to the territory again when space competitors were introduced; both individual and kin recognition have been demonstrated in *N. pulcher* [75,76]. At the ultimate level, such sharing of resources and tasks between breeders and offspring may be explained by kin selection. In contrast, there is no scope for kin selection in our study as the presented conspecifics were neither related nor familiar to the breeders. Furthermore, the ecological challenge we used was predation pressure on offspring or adults. Predation risk as an ecological cause of the acceptance of alien immigrants into groups of cooperative breeders was hitherto unknown. We argue that strategic group size adjustments to ecological requirements might be more common than appreciated. More generally, the effects of predation pressure on social interactions might be much more important than currently acknowledged.

Apart from perceived predation risk, the size difference between female breeder and the potential immigrant influenced the probability to accept a helper, whereas absolute immigrant size and the relation to the size of the male breeders had no influence on the probability of being accepted in the territory. This corroborates results from previous studies suggesting that the potential costs for breeders caused by subordinate group members increase with the latter's size [19,30,31,44]. Subordinates in our experiment were randomly chosen from a pool of fish on the verge of sexual maturation and therefore included both sexes. This might suggest that costs of subordinates are not primarily due to

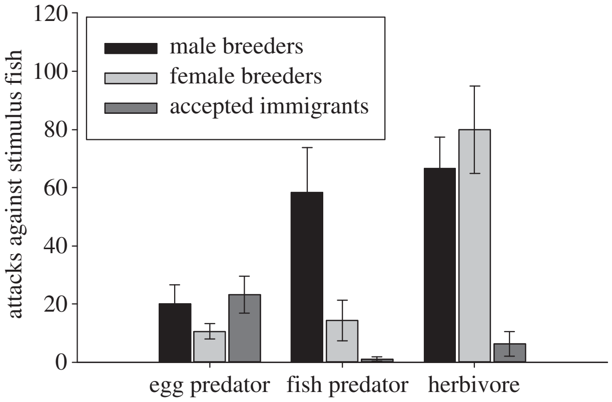


Figure 3. Mean and s.e. of breeder attacks ($N = 100$; attack rates of 50 male and 50 female breeders) and of attacks of accepted immigrants ($N = 38$) displayed against the respective stimulus fish. For statistical results see table 1*c*–*e*.

female–female competition as shown in other cooperatively breeding vertebrates [77,78]. Instead, regardless of the sex of the subordinates, individuals that are only slightly smaller than female breeders might induce higher potential costs to the pair, including for example an increased risk of egg cannibalism, as the submissive status of large helpers is an important precondition for them to care for eggs instead of eating them [79]. Unlike in cooperatively breeding mammals, where eviction is under female control [33,77], in *N. pulcher* both males and females participate in regulating group size [80]. Generally, the potential costs caused to breeders by opposite-sex subordinates are presently not well understood in cooperatively breeding vertebrates.

It seems surprising that the herbivore intruders were attacked very often by the pair, especially by female breeders. It has been shown that in *N. pulcher* attack rates are contingent on the risk individuals face when defending the territory [31,45]. This might be responsible for the high attack rates observed in breeders: as the risk is much smaller when attacking a herbivore than a fish predator, high attack rates on these intruders might reflect a low cost, low benefit strategy, as the risk of injury is probably negligible. The high attack rates against herbivore intruders might provide some insight into the cognitive mechanisms involved in the experimentally enhanced immigrant acceptance, implying that simple ‘attack-counting’ of breeders to determine the need for help is not responsible for the acceptance of additional group members. Rather, it seems that the presence of predators *per se*, regardless whether a risk to current group members or future eggs and larvae, raises the tolerance towards subordinate conspecifics.

It is yet unclear whether the recognition of threat is innate or learned. However, the fact that the fish showed adequate responses to predators even though all *N. pulcher* used in our experiment had never had direct contact to predators and herbivores before suggests that predator recognition in this species is innate and independent of learning. It is presently unknown which cues *N. pulcher* use to recognize predators. In the experiments both visual and olfactory cues could be used. If olfactory cues were important, they cannot include *Schreckstoff* or the smell of digested conspecifics (cf. [81]), as no conspecific was harmed by a predator during the experiment and all stimulus fish were fed on a flake food diet. This topic will be scrutinized in future studies.

5. Conclusions

Environmental conditions determine the cost–benefit ratio of accepting additional group members. This study shows that social interactions in a highly social vertebrate are contingent on the perceived risk of predation. Specifically, our experiment suggests that in *N. pulcher*, (i) enhanced predation risk increases the propensity to accept unknown and unrelated immigrants; (ii) predation pressure on group members and eggs has similar effects despite diverging benefits derived from additional group members; and (iii) immigrant acceptance is raised also when the potential benefit from receiving additional help (i.e. defence against potential predators of eggs and larvae) occurs only in the future.

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