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Reproductive sharing in relation to group and colony-level attributes in a cooperative breeding fish

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The degree to which group members share reproduction is dictated by both within-group (e.g. group size and composition) and between-group (e.g. density and position of neighbours) characteristics. While many studies have investigated reproductive patterns within social groups, few have simultaneously explored how within-group and between-group social structure influence these patterns. Here, we investigated how group size and composition, along with territory density and location within the colony, influenced parentage in 36 wild groups of a colonial, cooperatively breeding fish *Neolamprologus pulcher*. Dominant males sired 76% of offspring in their group, whereas dominant females mothered 82% of offspring in their group. Subordinate reproduction was frequent, occurring in 47% of sampled groups. Subordinate males gained more paternity in groups located in high-density areas and in groups with many subordinate males. Dominant males and females in large groups and in groups with many reproductively mature subordinates had higher rates of parentage loss, but only at the colony edge. Our study provides, to our knowledge, the first comprehensive quantification of reproductive sharing among groups of wild *N. pulcher*, a model species for the study of cooperation and social behaviour. Further, we demonstrate that the frequency of extra-pair parentage differs across small social and spatial scales.

1. Introduction

In group-living species, reproductive conflict can exist at multiple levels of the social structure. Group members may disagree over the distribution of reproduction within the group, as dominant individuals seek to monopolize reproduction while subordinate group members attempt to parasitize dominant reproduction, potentially facing punishment or eviction when doing so [1,2]. Individuals within a group may also come into conflict when group members mate with neighbouring individuals, as the offspring of neighbours may parasitize the resources and parental care of current group members [3]. Both within-group factors, such as group size and composition, and between-group factors, such as the density and location of neighbouring groups, influence the ability of individuals to pursue reproduction within their group [4,5] as well as pursue reproductive opportunities with neighbouring individuals [6,7]. Therefore, it is difficult to understand variation in individual behaviour or reproductive success without exploring how both within-group and between-group social structure affect the quality and quantity of reproductive opportunities.

Within-group attributes can influence the degree of reproductive sharing within the group (reproductive skew [1,2]) by altering the ability of dominant individuals to skew reproduction in favour of their own fitness interests. For

example, dominants may be less effective at reproductively suppressing subordinate reproduction when there are many same-sex subordinates acting as reproductive competitors [4,5], or when these same-sex subordinates are close in size to the dominant [8]. Furthermore, the frequency of extra-pair parentage in a group may be related to the size difference between the socially bonded male and female; males who are much larger than their socially bonded female may be better at preventing the female from reproducing with other males [9] or females with larger, potentially higher quality males may be less inclined to pursue extra-pair matings [7].

Colony-level factors can also have a profound influence on reproductive dynamics. High densities of neighbouring territories facilitate intergroup forays, providing females with opportunities to mate with neighbouring males or to lay eggs in other female's territories [10]. Further, competition with neighbours may be intense in densely inhabited areas and it may not always be possible to prevent one's social mate from mating with a neighbour [10]. In addition to density, the spatial location of a territory relative to other territories may influence reproductive patterns. Territories on the edge of a colony tend to be more exposed to predators [11,12]. If individuals occupying these edge territories must perform more predator defence or practice more vigilance, they may have less time and energy available for reproductive activities [13]. Additionally, because individuals from edge territories may be inferior competitors relative to individuals in the colony centre [14], high-quality individuals may exploit poor-quality competitors and reproduce with their socially bonded mate [15]. While it has been well established that territory location can have a significant impact on the number of offspring produced [12,16,17], far less is known about how the spatial location of a territory in relation to other territories influences extra-pair parentage.

Finally, within-group dynamics are not independent of the dispersal and reproductive opportunities offered by neighbouring groups [1,2,18]. An individual's ability to control its mate's activity is probably reduced when there is an increased availability of high-quality extra-pair mates in neighbouring groups [10]. Similarly, when there are a high number of opportunities to mate outside of the social group, dominants may be less concerned with suppressing subordinate reproduction within their own group. Further, if subordinates risk eviction to reproduce within the group, the willingness to engage in reproduction may rise if there are many groups to disperse to, or if the quality of their group is low relative to surrounding groups [18–20]. Hence, to better understand why and how patterns of reproductive sharing arise, within- and between-group factors need to be considered in tandem.

To determine how between-group traits, within-group characteristics and the interaction between these two levels of social structure impact rates of extra-pair parentage, we examined within-group and colony-level demographics in relation to parentage in 36 wild groups of *Neolamprologus pulcher*, a cooperatively breeding cichlid native to Lake Tanganyika, East Africa. These fish form colonies of 2–200 territorial groups, each with a dominant pair and 1–15 subordinate group members who help raise the offspring of the dominant pair [21]. Individuals primarily interact with other members of their own social group and those belonging to neighbouring social groups located within a 3 m radius [22,23]. Individuals strongly prefer to settle on territories in the centre of the colony and will often remain subordinates

on centre territories rather than become dominants on edge territories [22]. While there is physiological evidence of reproductive suppression in subordinates of both sexes [24,25], previous laboratory studies have shown that subordinate males and females can reproduce within their home groups [5,25–28] and one study found evidence of subordinate female reproduction in the wild [29]. Here, we investigated the possibility that dominants may lose parentage to neighbours, to subordinate group members, or to both.

We predicted that rates of extra-pair paternity (EPP) would be greater on the edge of the colony and at higher densities [6,7]. By contrast, we predicted that extra-pair maternity (EPM) would be low regardless of territory location or density, because females in this species can recognize and destroy competitor eggs [27]. Regarding within-group characteristics, we predicted that parentage loss would increase as group size and the number of same-sex subordinates increased [4,5] and that subordinates closer in size to the dominant would be more likely to reproduce [8]. Finally, we predicted that a larger size difference between the dominant male and female would allow the dominant male to exert more control over group dynamics, facilitating subordinate or neighbouring female reproduction and suppressing subordinate or neighbouring male reproduction [9].

2. Material and methods

(a) Study site and collection

Between February and April 2013, we sampled 36 *N. pulcher* groups found in Kasakalawe Bay, Lake Tanganyika, East Africa (8°46′ S; 31°46′ E) using SCUBA. Groups all had free-swimming offspring and were located in seven different colonies or subpopulations ranging in depth between 11 and 13.5 m. In order to minimize disturbance in the colony the sampled groups comprised less than 10% of the total number of groups in these colonies. Colonies consisted of a clustering of distinct social groups each defending a territory. Colonies are separated from each other by large open expanses of sand and rocky rubble uninhabited by *N. pulcher* [21,30]. Each group's territory was defined as the area of rocks defended by the dominant male and female, who are the largest individuals in the group [21]. The dominant and subordinate fish were identified as part of the focal group if they swam repeatedly under the territory rocks (shelter) without eliciting aggression from other fish within the territory boundaries. We measured territory size for each focal group and mapped the distance to all conspecific neighbours within a 3 m radius. A group was considered to be on the edge of the colony if half or more of that group's territory bordered an unoccupied area, with no other conspecific group within 10 m.

Using fence nets and hand nets, we captured all individuals in these 36 groups that were close to sexual maturity (more than 30 mm standard length (SL): the tip of the snout to the base of the caudal fin [31]). We then injected 20 ml of a clove oil mixture (one part clove oil; three parts 70% ethanol; one part water) into the brood chamber (a central rock used for breeding and shelter) to euthanize any free-swimming young (less than 10 mm SL). Groups breed year round in this species, and young collected for this study were all estimated to be two to six weeks old. We brought all the collected fish to the surface, where we measured adult body mass (to nearest 0.001 g) and body length (SL to nearest 0.01 mm). Mature fish were euthanized by immersion in a lethal concentration of benzocaine and the gonads were removed from adults and weighed. The entire carcass of free-swimming young

and a section of the dorsal fin from adult fish were preserved with 95% ethanol for parentage analysis.

(b) Parentage analysis

We analysed parentage in 36 groups (24 groups from the centre and 12 groups from the edge of a colony) with a total of 397 offspring (mean: 11.0 ± 0.8 s.e. offspring per group). We genotyped adults and young using six loci previously used on this species [5,29] (US783 [32]; Tmo11, Tmo13, Tmo25 [33]; LOC101 [34]; UME003 [35]). We extracted genomic DNA from preserved fin clips and young (QIAGEN DNeasy Blood and Tissue Kits) and used it in multiplexed PCR reactions, which involved six primer pairs end-labelled with the fluorescent dyes (FAM, HEX and NED; QIAGEN Multiplex Kit). We amplified samples using a Eppendorf thermocycler with a touchdown program set to the following parameters: 15 min at 95°C; 8 cycles of 30 s at 94°C, 90 s at 55°C (decreasing 0.5°C per cycle), 60 s at 72°C; 21 cycles of 30 s at 94°C, 90 s at 50°C, 60 s at 72°C; 30 min at 60°C; 60 s at 10°C. We ran amplified samples on an ABI DNA sequencer (3100 Genetic Analyzer) and scored the profiles using GENEMAPPERANALYSIS software.

We used CERVUS v. 3.0 to assign maternity and paternity at the 95% confidence level. The loci were highly variable with an average of 25 alleles per locus (see the electronic supplementary material, table S1). One locus (LOC101) significantly deviated from Hardy–Weinberg equilibrium owing to a high number of null alleles and so we removed it from our analyses. The combined exclusion power of the remaining five loci averaged 0.998 for a single parent and over 0.9999 for a parent pair.

(c) Statistical analysis

Most offspring (98.2%) genotyped had at least one assigned parent in the social group, indicating that both young and group members had been correctly identified and that, unlike some other cichlid species, this species does not appear to adopt unrelated fry [36]. When two of our 36 focal groups were less than 3 m apart, we tested adults from the other, nearby focal group as potential parents. When young could not be assigned to any collected potential father or mother, we determined the minimum number of mothers or fathers that had contributed to that group's parentage by counting the number of alleles at each locus that did not come from the assigned mothers or fathers collected with the brood. As a conservative estimate, we assumed all unknown parents were heterozygotes and contributed two alleles per locus.

We examined the factors correlated with the number of offspring assigned to the dominant male/female within the sampled group and to the subordinates within the sampled group (generalized linear mixed effects models; GLMER with Poisson distribution; R v. 3.0.2, glmmadmb package [37,38]). We also tested factors influencing the number of parents contributing to a brood using cumulative link models (CLM) in the ordinal package [39]. For all models, we tested the fixed effects of location within the colony (centre versus edge), density of neighbouring groups (number of conspecific groups within 3 m), group size, number of same-sex subordinates within the group, number of offspring collected (to control for variation in brood size) and relative size difference between the dominant pair ([dominant male SL − dominant female SL]/dominant male SL). The colony of each focal group was included in GLMER models as a random effect, but could not be used in a cumulative link mixed model because the model would not converge. For all models, two-way interactions were tested and non-significant interactions were removed from the models. Models for males and females were run separately. None of the within-group characteristics (e.g. group size, dominant size) were significantly different between groups from the centre
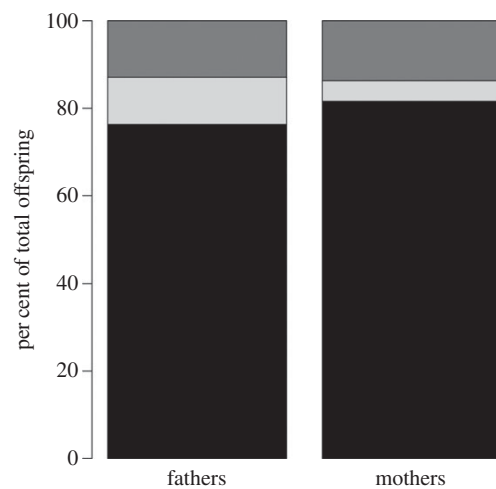

Figure 1. The per cent of offspring (pooled across all 36 sampled groups) belonging to the dominant male or female (black), and to subordinate males and females in the social group (light grey). The per cent of all instances of extra-group reproduction are shown in dark grey and represent, a combination of reproduction assigned to known individuals outside the sampled group and reproduction that was unable to be assigned.

versus edge of the colony, nor did they vary with the density of neighbouring groups (electronic supplementary material, table S2). Density also did not vary with location within the colony (linear mixed effects (LME): $F_{1,28} = 1.16$, $p = 0.29$).

It is possible that dominants were misidentified in the seven groups in which the dominants gained no parentage. In all other groups, dominants gained more than 50% of parentage and it is unlikely they were misidentified. In one of the five groups where the dominant male gained no paternity, two extremely small subordinate males (30 mm and 32 mm SL) gained all paternity in that group. In two additional groups, extensive behavioural observations confirmed the identity of the dominant male. Therefore, we reran our analyses excluding the other four groups with no dominant paternity ($n = 2$) or maternity ($n = 2$). Our results were largely robust to these exclusions (see the electronic supplementary material, tables S3 and S4) and therefore the full dataset is presented below.

3. Results

(a) Parentage loss

Across our 36 study groups, dominant males fathered 76.3% of collected offspring (303 out of 397 offspring genotyped). The dominant male fathered all offspring in 12 groups, the majority of offspring in 19 groups (mean paternity $\pm$ s.e: $72.8\% \pm 3.4$), and no offspring in five groups. Of the 94 offspring that could not be assigned to the dominant male collected with the social group, 34 were assigned to a subordinate male in the same social group (mean $10.8\% \pm 3.7$ s.e. of offspring within their social group), four were assigned to a subordinate male from another sampled group, one was assigned to a dominant male from another sampled group, and 55 could not be assigned to any male sampled (figure 1). These unassigned offspring were probably fathered by males in groups that we did not sample or by males within the group that had been recently evicted or eaten by a predator. The number of fathers per brood ranged from 1 to 4 (mean: 2.1 ± 0.2 s.e.).

The dominant females mothered 81.6% of offspring (324 out of 397 offspring genotyped). The dominant female

Table 1. Allocation of paternity within groups. (Test statistics (with d.f.) and p-values from full models measuring the effect estimates of location (centre versus edge), density of neighbouring groups, group size, relative size of dominant male to dominant female ([dominant male SL − dominant female SL]/dominant male SL), and the number of male subordinates on the number of offspring assigned to dominant and subordinate males within the sampled group (GLMER) and number of fathers contributing to the brood (CLM). Total number of offspring within each brood was included as a fixed effect to control for variation in brood size. Asterisks indicate significance, assessed at $\alpha = 0.05$.)

predictors	dominant male reproduction		subordinate male reproduction		no. fathers	
	test stat.$_{22}$	p-value	test stat.$_{22}$	p-value	test stat.$_{29}$	p-value
location	3.22	0.001*	−2.92	0.004*	1.95	0.05*
density	−1.06	0.29	2.04	0.04*	2.04	0.04*
group size	1.18	0.24	−1.89	0.06	1.13	0.26
size difference	1.69	0.09	−1.28	0.20	0.21	0.83
male subordinates	−0.39	0.70	3.24	0.001*	1.11	0.27
offspring	7.05	<0.001*	−1.65	0.10	0.21	0.83
location × group size	−3.59	<0.001*	3.16	0.002*	—	—

collected with the focal group was the mother of all offspring in 18 of the social groups, the majority of offspring in 16 groups (mean maternity ± s.e: 75.2% ± 5.4), and no offspring in two groups. Of the 73 offspring not assigned to the dominant female, 23 were assigned to a subordinate female in the same group (mean 4.7% ± 1.6 s.e.), two were assigned to a dominant female from another sampled group, and 48 were not assigned to any female sampled (figure 1), meaning that these offspring were probably mothered by females in groups that we did not sample or by females within the group that were recently evicted or eaten by a predator. The number of mothers per brood ranged from 1 to 4 (mean: 1.6 ± 0.1 s.e.). The degree of maternity loss across social groups was not correlated to the rate of paternity loss (LME: $F_{1,28} = 0.19$, $p = 0.85$).

(b) Subordinate reproduction

Subordinate males reproduced in almost a third of the sampled groups (11 out of 36) and subordinate females reproduced in a quarter of groups (9 out of 36). Of the reproductively mature subordinates genotyped, 35% of male subordinates (13 out of 37 males) and 19% of female subordinates (9 out of 47 females) achieved some degree of reproductive success. Subordinate females as small as 36 mm SL reproduced and males as small as 30 mm SL reproduced, which for males is below the average size previously reported for sexual maturation [30]. The likelihood of a male subordinate reproducing was not influenced by his body size relative to the dominant male ([SL dominant − SL subordinate]/SL dominant; generalized linear models; GLM with binomial error distribution: $Z_{24} = 0.95$, $p = 0.34$); however, female subordinates were more likely to reproduce if they were close in size to the dominant female (GLM: $Z_{35} = -2.22$, $p = 0.03$). There was no influence of relative gonad size (gonad mass relative to body mass, GSI) on whether a subordinate of either sex reproduced (GLM: males: $Z_{24} = 1.06$, $p = 0.29$; females: $Z_{35} = -0.82$, $p = 0.41$).

(c) Group and colony-level factors related to parentage loss

Dominant males lost significantly more paternity and subordinate males gained significantly more paternity in larger groups, but this occurred only in territories on the edge of

the colony (table 1: location by group size interaction). There was no strong influence of group size on dominant and subordinate paternity in groups in the centre of the colony (table 1). Subordinate males also gained more paternity in higher density areas and in groups with more males (table 1). The number of fathers per brood increased with the density of neighbouring groups and was higher on the edge of the colony compared with the centre (table 1). Groups in high-density areas and on the edge of the colony also had a higher number of offspring that could not be assigned to any collected male group member (GLMER; density: $Z_{29} = 1.96$, $p = 0.05$; location: $Z_{29} = 2.97$, $p = 0.003$), suggesting that neighbouring males sired a larger proportion of offspring in those areas. Although gonadal investment (GSI) of dominant males did not vary with territory density, males on edge territories had relatively larger gonads than males with territories in the centre of the colony (LME; location: $F_{1,33} = 4.49$, $p = 0.04$; density: $F_{1,33} = 1.39$, $p = 0.25$).

On the edge of the colony, groups with many subordinate females had dominant females that lost more maternity, subordinate females that gained more maternity and more mothers per brood compared with edge groups with fewer female subordinates (figure 2a and table 2: location by female subordinate interaction). By contrast, centre groups with a high number of subordinate females had dominant females that retained more maternity, subordinate females that gained less maternity, and fewer mothers per brood compared with centre groups with fewer female subordinates (figure 2b and table 2). Interestingly, dominant females who were much smaller than the dominant male retained a larger portion of the maternity of their brood compared with dominant females who were close in size to the dominant male (table 2). This result was driven by differences in dominant male size, as females paired with larger dominant males suffered less loss of maternity (figure 3; GLMM; $Z_{21} = 2.05$, $p = 0.04$).

4. Discussion

EPP and EPM were common in this study, accounting for 24% and 18% of the total number of sampled offspring, respectively. For both males and females, extra-pair offspring
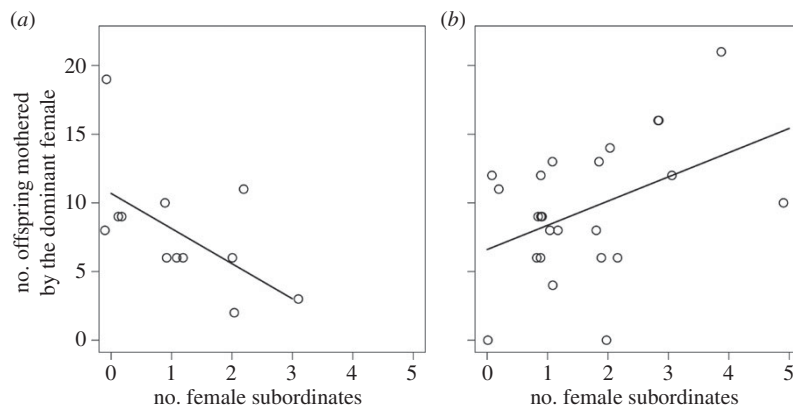
Figure 2. (a) In the 12 groups on the edge of the colony, the number of offspring mothered by the dominant female decreased as the number of female subordinates in the group increased (GLMER: $Z_6 = -2.97$, $p = 0.003$). (b) By contrast, in the 24 groups in the centre of the colony, the number of offspring mothered by the dominant female increased as the number of female subordinates in the group increased (GLMER: $Z_{16} = 3.38$, $p < 0.001$).

Table 2. Allocation of maternity within groups. Test statistics (with d.f.) and p-values from full models measuring the effect estimates of location (centre versus edge), density of neighbouring groups, group size, relative size of dominant male to dominant female ([dominant male SL − dominant female SL]/dominant male SL), and the number of female subordinates on the number of offspring assigned to dominant and subordinate females within the sampled group (GLMER) and the total number of mothers contributing to the brood (CLM). Total number of offspring within each brood was included as a fixed effect to control for variation in brood size. Asterisk indicate significance, assessed at $\alpha = 0.05$.

predictors	dominant female reproduction		subordinate female reproduction		no. mothers	
	test stat.$_{22}$	p-value	test stat.$_{22}$	p-value	test stat.$_{29}$	p-value
location	1.89	0.06	−2.85	0.004*	−2.75	0.006*
density	0.29	0.77	0.87	0.38	0.29	0.77
group size	−0.74	0.46	1.33	0.18	0.22	0.83
size difference	1.96	0.05*	−1.05	0.29	−1.15	0.25
female subordinates	1.89	0.06	−2.54	0.01*	−2.48	0.01*
offspring	4.70	<0.001*	4.16	<0.001*	2.90	<0.001*
location × female subordinates	−2.41	0.003*	3.46	<0.001*	3.34	<0.001*

were sired by subordinates within the group as well as by individuals from neighbouring groups. Both within-group characteristics, including the size of the dominant male, and between-group characteristics, such as the density of neighbouring groups, significantly influenced reproductive dynamics within groups. Further, the effect of some within-group characteristics, such as group size, varied with colony-level characteristics. Collectively, these results suggest that understanding of the reproductive dynamics within colonial groups requires comprehension of both within- and between-group social dynamics.

This study provides strong evidence of extensive subordinate reproduction in wild groups of this well-studied fish species. We uncovered high levels of subordinate reproduction, with 35% of collected male subordinates and 19% of collected female subordinates achieving some degree of reproductive success. Previous studies based on much smaller sample sizes [29,40] found no occurrences of subordinate male reproduction and only one occurrence of subordinate female reproduction in the wild, leading to the mistaken conclusion that subordinate reproduction is rare in free-living *N. pulcher* groups.

High levels of subordinate reproduction in a cooperatively breeding system call into question current explanations for the fitness benefits of helping in these fish. If subordinates obtain high levels of reproduction, what is perceived to be subordinate alloparental care may in fact represent direct parental care [21]. Further, if subordinates reproduce within their own groups, then lost reproductive opportunities resulting from delayed dispersal, considered to be one of the main costs of helping [21], may have previously been overstated. Our study demonstrates that the evolution of apparent helping behaviour in *N. pulcher* may be at least partly explained by direct reproductive benefits. Although some cooperatively breeding species have higher levels of subordinate reproduction than those reported in this species, this degree of subordinate reproduction is rare for cooperative breeders, as subordinates in many cooperatively breeding species are reproductively suppressed, either behaviourally or physiologically, by dominants [41]. In birds, the evolution of cooperative breeding is associated with lower rates of extra-group parentage [42,43], but cooperative breeding can be maintained even in highly promiscuous species if subordinates receive direct benefits while helping in the group [44]. Given the high level
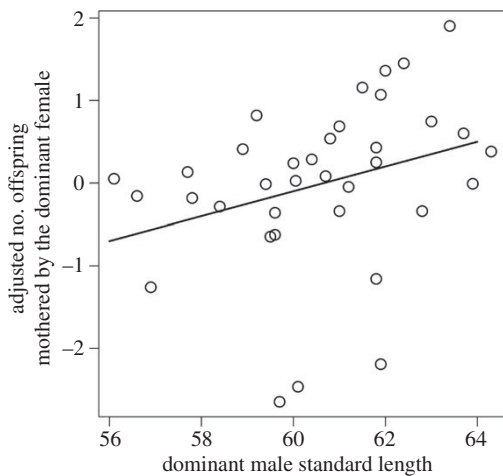
Figure 3. Across all 36 sampled groups, dominant females mothered more offspring (after controlling for variation in brood size) when they were mated with a large male, both in terms of absolute size (SL, as shown in this figure) and in terms of size relative to the dominant male (table 2). Data presented are least squared means of the regression model testing predictors of the number of offspring mothered by the dominant female.

of extra-group parentage found in this study, some baseline subordinate reproduction may be necessary for assuring continued subordinate help and membership in the group [45].

The social environment can also determine the level of within-group subordinate reproduction by altering the ability and motivation of subordinates to reproduce [20,46]. On the colony edge, the portion of the brood mothered by subordinate females increased as the number of female subordinates within the group increased; however, in the colony centre, groups with many female subordinates actually had comparatively less subordinate female reproduction. Similarly, subordinate males reproduced more frequently in larger groups, but only on the edge of the colony. Compared with dominants in the colony centre, dominants on the edge of the colony may be less capable of suppressing subordinate reproduction or they may concede more reproduction to subordinates because they are more reliant on subordinates for defence against predators [45].

Alternatively, subordinates in central territories may choose not to reproduce, as getting evicted following reproduction [26] would result in losing the opportunity to inherit a high-quality territory in the centre of the colony. This would be particularly costly for subordinates in large groups, which are more productive and more likely to persist from year to year [47,48]. However, if there are lower fitness benefits to inheriting low-quality territories on the colony edge [22], the benefits of reproducing for subordinates may outweigh the costs of getting evicted due to reproduction. Similarly, subordinate males may reproduce more frequently in denser areas because eviction may be less costly when there are a high number of potential groups to join. Further, increased reproduction by neighbouring males may mean that subordinates on the colony edge and in denser areas are less related to the offspring in their group compared with subordinates in the centre or in less dense areas. Therefore, subordinates in the centre or less dense areas may gain greater indirect fitness benefits, future fitness benefits, or both, by providing alloparental care, compared with subordinates on the edge or in denser areas.

In addition to high rates of subordinate reproduction, we found evidence of EPM in about half of the sampled groups. Dominant females paired with large males mothered a larger portion of offspring compared with dominant females paired with smaller males. Across a variety of taxa, larger and older males are higher quality mates, have more reproductive success and are more likely to be extra-pair mates [15,49–51]. Dominant females paired with smaller males may be more likely to pursue mating opportunities with higher quality males in neighbouring groups and spend less time guarding against reproductive competitors [10]. Large dominant males may also be more successful at cuckholding neighbouring males and mating with females in neighbouring territories. They may choose this strategy, rather than court females in their own territory, because reproduction of multiple females within a territory can increase within-group conflict [52,53], and siring offspring on other territories allows males to parasitize the care and resources of other individuals [3].

On the edge of the colony, a higher proportion of collected offspring were sired by males other than the collected dominant or subordinate males, suggesting that neighbouring males steal more paternity from a given resident male on the edge of the colony compared with the centre. Resident males on the edge of the colony may have a reduced ability to prevent other males from mating with their social mate, either due to decreased quality or to increased time spent vigilant against predators [11–14]; however, edge males may also adopt different mating strategies. In wild guppy populations (*Poecilia reticulata*), EPP is much more common in high-predation environments compared with low-predation environments [54]. Experiments manipulating predation pressure in guppies found that, under perceived high-predation pressure, males reduce their courtship displays and sneak copulations more often [55], while females become less selective regarding potential mates [56]. This is probably because courtship displays and mating selection tend to attract predators [57]. This may also explain why males on the edge of the colony had the largest testes; edge males may invest substantially more in sneaking paternity in neighbouring nests compared with males in the centre.

Here, we provide support that both within- and between-group factors are linked to reproductive patterns in *N. pulcher*. Further, we found that the influence of within-group characteristics may depend upon colony-level social structure. Our results demonstrate that studies of reproductive dynamics within groups should consider the influence of neighbouring groups, which offer additional reproductive opportunities and can alter how individuals pursue reproductive opportunities within their own group. Our results suggest that individuals occupying lower quality edge territories may adopt different reproductive strategies to accommodate increased predation risk. Further, subordinates may attempt to reproduce when living in lower quality edge territories to compensate for lowered kin-selected benefits of alloparental care or the costs of living in a suboptimal habitat. We suggest that the patterns of extra-pair parentage and the selective pressures governing the pursuit of extra-pair parentage may vary over relatively small spatial and social scales. Further research exploring behavioural and reproductive exchanges within and between groups would be useful for elucidating the extent to which individuals vary their decisions based on the presence of neighbouring groups.

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