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Chapter 5

Predation risk mediates the anti-predator benefits of sociality and suppresses within-group conflict in a cooperatively breeding cichlid fish

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ABSTRACT

Social conflict is a repellent force in the evolutionary transitions to complex sociality. Thus, identifying the factors reducing such conflict is crucial in order to understand why and how such transitions occur. Predation risk, while thought to be a major factor selecting for group living, has generally been undervalued as a driver of complex sociality, despite the potential benefits of cooperation under high risk of predation. In the current study, we investigated whether predation risk leads to decreased social conflict, both within and between groups, in the cooperative breeder *Neolamprologus pulcher*. This highly social cichlid fish species lives in stable groups of a dominant breeding pair and several brood care helpers. We show that in nature, dominants reduce aggression towards subordinates under increased risk of predation, and that aggressive interactions between subordinates decline accordingly. Subordinates show reduced levels of submission and no changes in helping behaviour with increasing predation risk, indicating that this is not the cause of reduced aggression by dominants. In contrast, aggression between groups is independent of the level of predation risk. This coincides with significant fitness effects of the presence of subordinates in dependence of the levels of predation risk, whereas the presence of close neighbours did not affect reproductive output. Reduced aggression by dominants apparently serves to incentivize large subordinates, which are important for the defence against large predators, to remain in the group, despite the costs they inflict due to competition for resources and reproduction. We argue that that delayed dispersal by large subordinate might thus be driven by mutualistic benefits of cooperation under increased threat of predation. These results demonstrate the importance of trade-offs between predator protection and intra-group competition, highlighting the importance of predation risk for the evolution of complex social systems.

INTRODUCTION

The evolution of life on earth has been characterized by several key steps which involved previously self-replicating entities (e.g. genes, cells, individuals) to cooperate and form more complex units, which have been termed major evolutionary transitions (Smith & Szathmáry 1995). Several processes have been identified that are necessary for such transitions to take place, including group formation, benefits of cooperation, division of labour and suppression of conflict (West *et al.* 2015). Conflict often occurs when there are incompatible fitness interests between individuals, and can diminish, or even negate, the benefits obtained through cooperation. Consequently, the factors that reduce conflict have received much attention from evolutionary ecologists (Krause & Ruxton 2002; Bourke 2011). Kin selection, i.e. fitness effects of genes accrued through its effects on relatives carrying the same genes (Hamilton 1963, 1964), can reduce conflict between individuals and thereby promote transitions to sociality (West-Eberhard 1975; Clutton-Brock 2002; Briga *et al.* 2012; Bourke 2014). However, it has limited explanatory power in cases where cooperation occurs mainly between non-relatives. Thus, alternative hypotheses are necessary to explain limited social conflict and the evolution of cooperation in groups consisting mainly of unrelated individuals.

Competition for finite resources (i.e. food or reproduction) is considered to be one of the predominant costs of group living (Alexander 1974; Reeve 2000; Shen *et al.* 2014). This competition is usually expressed in the form of aggression, which is aimed at obtaining a larger share of such resources at the expense of others, leading to social conflict (Shen *et al.* 2014). In social groups where some individuals (i.e. dominants) have control over group membership of others (i.e. subordinates) through the use of aggression (Johnstone & Cant 1999), conflict can lead to evictions. Social conflict and resulting eviction are common features of many cooperatively breeding mammals (e.g. Clutton-Brock *et al.* 2001; Cant *et al.* 2010), birds (e.g. Webster 1994; Dunn *et al.* 1995) and fishes (e.g. Taborsky 1985; Balshine-Earn *et al.* 1998; Fischer *et al.* 2014). Additionally, dominants can use aggression to force subordinates to provide (more) help, potentially leading to negotiations about 'optimal' levels of help (Gaston 1978; Quiñones *et al.* 2016). Conflict can also occur between subordinates in the same group, for instance over access to food or position in the hierarchy (Field & Cronin 2007). Regardless of the function or source of aggression, subordinates should disperse voluntarily when the costs (e.g. levels of aggression received and help provided) of being in the group exceeds its benefits (e.g. protection against predators). Social conflict and aggression are therefore expected to decrease when the benefits of having additional group members and/or cooperation, are high.

Predation risk is a major ecological factor selecting for group living through passive benefits, such as increased risk dilution or predator confusion (Wrona & Dixon 1991; Lehtonen & Jaatinen 2016), or through active cooperation between group members, like joint vigilance or predator defence (Heg *et al.* 2004a; Bonte *et al.* 2012; Groenewoud *et al.* 2016). Furthermore, predation risk can favour the clustering of social units into colonies, when neighbours reduce the risk of predation, or the costs associated with anti-predator defence (Rolland, Danchin & de Fraipont 1998; Schädelin, Fischer & Wagner 2012; Jungwirth *et al.* 2015a). The anti-predator benefits of having larger groups, or more neighbours are ultimately expected to lead to increased survival or reproductive success (Krause & Ruxton 2002; Jungwirth & Taborsky 2015). Despite these benefits, having close neighbours also results in conflict, when groups compete over space or resources (Krause & Ruxton 2002). Groups are therefore expected to invest less in such competition and cooperate more when neighbours provide benefits, such as increased defence against predators (Krams *et al.* 2010). Predation risk is therefore expected to play an important role in reducing conflict and promoting cooperation between individuals living in social groups, and facilitate the transition to complex sociality.

Here, we investigate whether predation risk is associated with reduced conflict both within and between groups, in the highly social, cooperatively breeding cichlid *Neolamprologus pulcher*. *N. pulcher* is endemic to Lake Tanganyika, where it occurs in highly variable habitats along the sublittoral zone between 2-45 m of depth (Konings 1998; Groenewoud *et al.* 2016). Groups consist of a dominant breeding pair and one to 26 subordinates (median = 5 subordinates, this study) of different sizes and sex, which jointly defend a territory that is used for both shelter and breeding (Taborsky & Limberger 1981; Taborsky 1984). Due to frequent breeder turnover, older and therefore larger subordinates are mostly unrelated to the dominants in their group (Dierkes *et al.* 2005). Low relatedness, larger body size and the fact that these individuals are often sexually mature, makes them a bigger threat to the dominants and increases the likelihood of conflict compared to smaller helpers that cannot reproduce and are mostly related to the breeders. However, larger helpers are also important to defend against large piscivorous predators, and previous studies have shown that they improve the survival of individuals in the group (Heg & Taborsky 2010). Subordinates in *N. pulcher* have been shown to provide help in order to be tolerated inside the relative safety of the territory (i.e. “pay to stay”; Gaston 1978; Bergmüller *et al.* 2005b). When the costs of eviction are higher, such as under elevated predation risk, this could favour subordinates to provide more help in order to prevent being evicted (Fischer *et al.* 2014). Previous studies have indicated that predation risk is an ecological constraint leading to the delayed dispersal of larger subordinates, and consequently, a higher number of large subordinates in groups under high risk of predation (Heg *et al.* 2004a; Groenewoud *et al.* 2016). These patterns have mainly been

explained in the context of increased costs of dispersal under elevated predation risk, but reduced aggression by dominants to incentivize larger subordinates to remain in the group has not yet been explored. On top of the benefits enjoyed by having subordinates, groups also benefit from increased anti-predator defence by having close neighbouring groups (Jungwirth & Taborsky 2015; Jungwirth *et al.* 2015a; Groenewoud *et al.* 2016). Predation risk should therefore increase the benefits of first order (i.e. groups) and second order (i.e. colonies) sociality and lead to reduced aggression at both levels of organisation.

In this study we address the following questions: (i) do (large) helpers and close neighbours provide fitness benefits under increased predation risk? (ii) Is conflict within- and between groups reduced under increased predation risk? (iii) Do large subordinates invest more in predator defence than small subordinates (i.e. is there division of labour)? (iv) Are potential reductions in conflict the result of changes in helping or submissive behaviours? Together, these results will shed light on the relative benefits of sociality for different individuals living under varying predation risk, and provide valuable insight into the role of predation risk as a factor to reduce conflict and facilitate transitions to complex societies.

METHODS

Study species and data collection

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 between 150 m and 22.45 km apart, with seven populations being within 9 km of each other and one population located about 20 km away. Population boundaries were established where no other territories were found within five meters of the outermost territories of the colony, except for two very large populations where artificial boundaries were established despite other territories being close by. We randomly selected 20-24 territories from each population and determined the group size and composition: fry (<0.5 cm), juveniles (0.5-1.5 cm), small helpers (1.6-2.5 cm), medium helpers (2.6-3.5 cm), large helpers (>3.5 cm), similar to Heg *et al.* (2004a). Dominant males and females could be easily distinguished from subordinates based on size and behaviour. 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). We measured the distance to the nearest neighbouring territory from the centre of each focal territory to the nearest five cm and counted the total number of territories present within a two meter radius.

Predation risk

We estimated predation risk in each population by counting the number of piscivorous predators (mostly *Lepidolamprologus elongatus* and *L. attenuatus*) along four transects of $10 \times 1 \text{ m}^2$. These are highly mobile predators, usually observed alone or in small groups moving through the 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. We repeated these scans between 6 and 10 times per population on different days and different weeks 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 ($>10 \text{ cm}$) *L. elongatus* and *L. attenuatus* per transect, similar to Groenewoud *et al.* (2016).

Behaviours

In each focal territory we observed the behaviours (sensu Taborsky & Limberger 1981; Taborsky 1984) of both breeders and one helper per size class (when present) for 7 minutes using a handheld computer (Psion Teklogix Workabout Pro-7527) running Noldus Pocket Observer (v3.0). We scored all aggressive behaviours (biting, ramming, mouth fighting, lateral displays, opercula spread and chasing) towards group members, neighbours and predators, and recorded the size class of the receiver. Furthermore, we recorded all territory maintenance (digging and removing debris from the territory), and submissive behaviours (bumping and tail quivers), and the time focal individuals spent inside the territory (i.e. within ca. 30 cm from the breeding shelter).

Statistical analyses

Reproductive success

We investigated whether the likelihood that a territory had produced offspring was dependent on the number of subordinates, territory density or predation risk in a generalised linear mixed model with a binomial error structure with a logit-link. We investigated the effects of different helper classes (i.e. large, medium and small helpers) separately, and for each helper class, we fitted five models representing different hypotheses (see Table S5.1) about the relationship between the numbers of subordinates, territory density and predation risk on whether a territory contained fry or juveniles (0/1). We included *Population ID* as a random effect in each model. We calculated Akaike weights and evidence ratios based on AICc values (Akaike 1973; Hurvich & Tsai 1989) to identify the model with the lowest out-of-sample deviance (Burnham & Anderson 2002; Burnham, Anderson & Huyvaert 2010). We then used this model to obtain parameter estimates for variables of interest. Parameter significance here and in all other models was obtained by likelihood ratio tests on nested models assuming a χ^2 -distribution (Zuur *et al.* 2009). In case two or more models had similar weights (i.e. were close in out-of-sample deviance), results from these models were also

investigated. All generalized linear mixed models were fitted with “lme4” in R (R Core Team 2016). Likelihood ratio tests were performed using the package “AICcmodavg” (Mazerolle 2013) and AICc values and Akaike weights were calculated using the “MuMin” package (Barton 2018). All models were checked for violations of model assumptions by visual inspections of residuals.

Within- and between group conflict

We investigated whether the likelihood of dominant aggression towards subordinates decreased with increasing predation risk by fitting whether aggression had occurred during our 7-minute observation (0/1) as a response variable in a generalised linear mixed model with a binomial error and a logit-link. Predation risk, the helper class aggression was directed to, the number of helpers and the total time spent in the home territory by the dominants combined were included as predictor variables. For each territory, we only included dominant aggression towards helper classes that were present in the territory based on our estimates of group composition (see methods). We fitted five models representing different hypotheses about the relationship between predictors (Table S5.2), and calculated Akaike weights based on AICc, as before, to identify the model with the lowest out-of-sample deviance. Similarly, we investigated changes in within-group aggression between subordinates by fitting whether subordinates showed aggression to each other (0/1) as a response variable in a generalised linear mixed model. Predation risk, helper size class, and the total number of subordinates were fitted as predictors. We fitted five models representing different hypotheses about the relationship between predictors (Table S5.2). In both the model investigating dominant aggression and subordinate aggression, we included *Territory ID* as a random effect to account for repeated measures of individuals within territories.

To analyse changes in between-group aggression, we fitted whether aggression had occurred (0/1) between individuals belonging to different territories as a response variable in a generalised linear mixed model with a binomial error and a logit link. We included predation risk, territory density and individual class as predictors and fitted an additional model, which also included the interaction between predation risk and territory density. We then calculated Akaike weights based on AICc and estimated parameter significance.

Division of labour

We fitted whether individuals showed either anti-predator defence behaviour or maintenance behaviour (0/1) in a generalised linear mixed model with a binomial error and logit-link. We included individual class and type of behaviour as predictors and fitted the interaction between these variables to allow for differences in the relative probability of anti-predator behaviour and maintenance behaviour between individuals belonging to dif-

ferent classes. We included *Population ID* and *Territory ID* as random effects to account for differences between populations and repeated measures of individuals within territories. We used linear hypothesis tests implemented in the package “phia” (De Rosario-Martinez 2015) to obtain contrasts between behaviours for all individual classes. Similarly, we investigated differences in the proportion of anti-predator defence relative to total helping behaviour (all maintenance and defence against heterospecifics) between different helper classes. We fitted the number of aggressive behaviours towards predators as a binomial response variable where the number of trials was equal to the total number of helping behaviours, and we included *Population ID* and *Territory ID* as random effects.

Helping and submission

We investigated whether total helping behaviour and submissive behaviours changed with predation risk by fitting whether an individual showed either helping or submission (0/1) as response variables in separate generalized linear mixed models with a binomial error and logit-link. We included predation risk and individual class as predictors and added *Population ID* and *Territory ID* as random effects. Additionally, for both response variables, we fitted models including the interaction between predation risk and individual class and calculated Akaike weights, as before.

RESULTS

Reproductive success

For models investigating the likelihood that a territory contained fry, there was considerable support for a model that included the interaction between the number of large helpers and predation risk ($AICc_{\text{weight}} = 0.59$; Table S5.1). Likelihood ratio tests based on this model indicated that the number of large helpers had a larger positive effect on the likelihood of having reproduced with increasing predation risk (mean \pm SE = 0.11 ± 0.05 , $\chi^2 = 5.27$, DF = 1, $P = 0.02$; Fig. 5.1). There was no significant relationship between territory density and the likelihood of having reproduced in the highest ranked model (mean \pm SE = 0.02 ± 0.03 , $\chi^2 = 0.36$, DF = 1, $P = 0.55$). However, the second ranked model ($AICc_{\text{weight}} = 0.20$; Table S5.1) suggested a possible three-way interaction between predation risk, the number of large subordinates and territory density ($\chi^2 = 3.20$, DF = 1, $P = 0.07$).

A model that included the interaction between the number of medium helpers and territory density on the likelihood that a territory contained fry had the highest support ($AICc_{\text{weight}} = 0.51$; Table S5.1). However, likelihood ratio tests indicated that the interaction between the number of medium helpers and territory density, was not significant (mean \pm SE = $0.04 \pm$

0.02, $\chi^2 = 3.39$, $DF = 1$, $P = 0.07$). This model and the second ranked model did indicate that there was a significant negative relationship between predation risk and the likelihood that a territory had offspring (mean \pm SE = -0.23 ± 0.09 , $\chi^2 = 4.54$, $DF = 1$, $P = 0.03$), but there were no effects of the number of medium helpers (mean \pm SE = 0.06 ± 0.10 , $\chi^2 = 0.34$, $DF = 1$, $P = 0.56$) or territory density (mean \pm SE = 0.02 ± 0.03 , $\chi^2 = 0.57$, $DF = 1$, $P = 0.45$).

The number of small helpers showed a stronger positive relationship with the likelihood of having reproduced under high predation risk (mean \pm SE = 0.11 ± 0.04 , $\chi^2 = 6.07$, $DF = 1$, $P = 0.01$), and this was supported by AICc weights, which was 7.5 times higher than the second best ranked model (AICc_{weight} = 0.75 vs 0.10; Table S5.1).

Within- and between group conflict

For dominant aggression towards subordinates, there was highest support for a model without interactions (AICc_{weight} = 0.48 vs 0.22 for the model including predation risk x helper class interaction) and this was supported by the lack of significance for this interaction ($\chi^2 = 2.56$, $DF = 2$, $P = 0.28$). Dominant aggression towards all helper classes decreased similarly with increasing predation (mean \pm SE = -0.29 ± 0.08 , $\chi^2 = 14.54$, $DF = 1$, $P < 0.001$; Fig. 5.2A), while overall levels of aggression differed between helper classes ($\chi^2 = 14.13$, $DF = 2$, $P < 0.001$). Aggression of dominants was less likely to occur towards medium helpers and small helpers than towards large helpers (medium vs. large helpers: mean \pm SE = -1.33 ± 0.41 ,

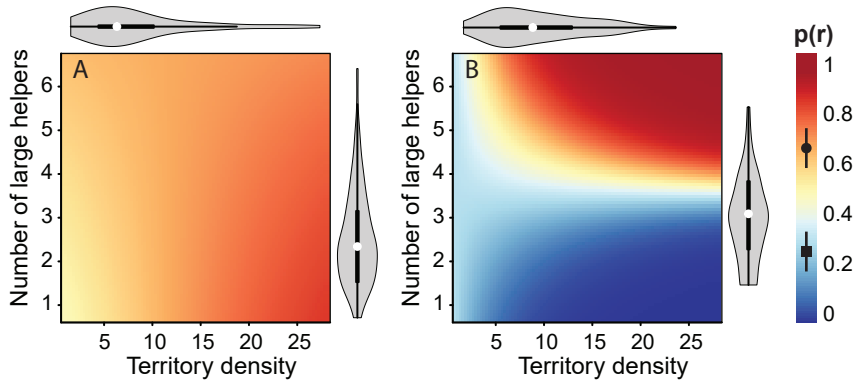


FIGURE 5.1 Probability that a territory contained fry or juveniles (< 1.5 cm) – indicating successful reproduction – depending on the number of large helpers and territory density under (A) low predation risk, or (B) high predation risk. The legend on the right indicates colours associated with the probability of successful reproduction $p(r)$. The closed circle and square in this legend give the mean (\pm SE) probability of reproduction under low and high predation risk, respectively. Violin plots show the distribution (median, interquartile range and density) of raw data for territory density (top) and the number of large helpers (side) for low ($<$ median) and high ($>$ median) predation risk.

$Z = -3.25$, $DF = 1$, $P < 0.01$; small vs. large helpers: mean \pm SE = -1.08 ± 0.40 , $Z = -2.72$, $DF = 1$, $P < 0.01$), and there were no differences between medium and small helpers (mean \pm SE = -0.25 ± 0.45 , $Z = -0.56$, $DF = 1$, $P = 0.57$). There was no significant relationship between the total time dominants spent in the territory and the likelihood they showed aggression towards subordinates (mean \pm SE = 0.67 ± 0.44 , $\chi^2 = 2.86$, $DF = 1$, $P = 0.09$).

Models investigating within-group aggression between helpers showed most support for a model without interactions ($AIC_{\text{weight}} = 0.55$ vs 0.24 for the second best supported model; Table S5.2). Aggression between helpers decreased significantly with increasing predation risk (mean \pm SE = -0.18 ± 0.06 , $\chi^2 = 10.85$, $DF = 1$, $P < 0.001$; Fig. 5.2B) and there were no differences in the likelihood of showing aggression between different helper classes ($\chi^2 = 0.73$, $DF = 2$, $P = 0.70$). The likelihood that helpers showed aggression towards other helpers increased with increasing group size (mean \pm SE = 0.09 ± 0.03 , $\chi^2 = 10.96$, $DF = 1$, $P < 0.001$).

The likelihood of between-group aggression became higher with increasing territory density (mean \pm SE = 0.10 ± 0.02 , $\chi^2 = 20.48$, $DF = 1$, $P < 0.001$), but was independent of the level of predation risk (mean \pm SE = 0.01 ± 0.05 , $\chi^2 = 0.04$, $DF = 1$, $P = 0.83$; Fig. 5.2C). There was limited support for an interaction between predation risk and density on between-group aggression as indicated by low weights for the interaction model ($AIC_{\text{weight}} = 0.72$ vs 0.28 for non-interaction vs interaction model, respectively). Individual classes differed significantly in the likelihood of showing aggression to neighbouring conspecifics ($\chi^2 = 58.09$, $DF = 4$, $P < 0.001$). Dominant females had the highest likelihood of showing aggression towards

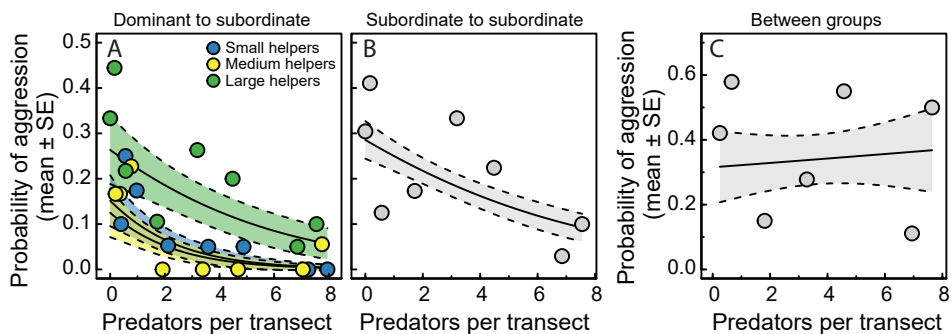


FIGURE 5.2 Counterfactual plots showing the relationship between predation risk and (A) dominant aggression to different classes of helpers, (B) aggression between subordinates in the same group and (C) aggression between individuals of different groups. Points in (A) represent mean probability of aggression for dominants to subordinates; slightly offset. In (B) points represent the mean probability of aggression between individuals of different groups. Solid and dashed lines are model predicted means (\pm SE). In (B) between-group aggression is plotted for dominant females.

neighbouring conspecifics, and this likelihood was not significantly different for dominant males (mean \pm SE = -0.41 ± 0.29 , $Z = -1.38$, $DF = 1$, $P = 0.17$), but lower for large helpers (mean \pm SE = -0.94 ± 0.31 , $Z = -3.00$, $DF = 1$, $P < 0.01$), medium helpers (mean \pm SE = -1.84 ± 0.39 , $Z = -4.75$, $DF = 1$, $P < 0.001$) and small helpers (mean \pm SE = -2.62 ± 0.48 , $Z = -5.48$, $DF = 1$, $P < 0.001$). Large helpers were more likely to show between-group aggression than small helpers (mean \pm SE = 1.68 ± 0.48 , $Z = 3.51$, $DF = 1$, $P < 0.01$), and tended to show more between-group aggression than medium helpers (mean \pm SE = 0.90 ± 0.39 , $Z = 2.28$, $DF = 1$, $P = 0.06$). The likelihood of between-group aggression did not differ between medium helpers and small helpers (mean \pm SE = 0.78 ± 0.52 , $Z = 1.50$, $DF = 1$, $P = 0.29$)

Division of labour

Individual classes differed significantly in the type of behaviours performed ($\chi^2 = 39.87$, $DF = 4$, $P < 0.001$; Fig. 5.3A). Small helpers were more likely to show maintenance than anti-predator defence behaviours (mean \pm SE = 1.86 ± 0.47 , $\chi^2 = 15.78$, $DF = 1$, $P < 0.001$). This pattern shifted with helper classes increasing in body size having a lower likelihood of maintenance behaviours and higher likelihood of anti-predator defence (medium helper vs small helpers: mean \pm SE = -1.50 ± 0.60 , $Z = -2.50$, $DF = 1$, $P = 0.01$; large helpers vs small helper: mean \pm SE = -1.72 ± 0.60 , $Z = -2.89$, $DF = 1$, $P < 0.001$; dominant female vs small helper: mean \pm SE = -2.32 ± 0.57 , $Z = -4.09$, $DF = 1$, $P < 0.001$; dominant male vs small helper: mean \pm SE = -3.65 ± 0.69 , $Z = -5.30$, $DF = 1$, $P < 0.001$). Dominant males had a higher likelihood of showing anti-predator defence than maintenance ($\chi^2 = 12.55$, $DF = 1$, $P < 0.01$). Additionally, we found that the proportion of anti-predator defence relative to other (allo-) parental care behaviours increased in individual classes with increasing body size ($\chi^2 = 39.80$, $DF = 4$, $P < 0.001$; Fig. 5.3B). Small helpers showed the lowest proportion of anti-predator defence, while this proportion was higher for medium helpers (mean \pm SE = 1.14 ± 0.50 , $Z = 2.29$, $DF = 1$, $P = 0.02$), large helpers (mean \pm SE = 1.66 ± 0.47 , $Z = 3.51$, $DF = 1$, $P < 0.001$), dominant females (mean \pm SE = 1.91 ± 0.45 , $Z = 4.24$, $DF = 1$, $P < 0.001$) and dominant males (mean \pm SE = 2.43 ± 0.47 , $Z = 5.22$, $DF = 1$, $P < 0.001$)

Helping and submission

The likelihood of showing submissive behaviours towards the dominants decreased with increasing predation risk (mean \pm SE = -0.41 ± 0.17 , $\chi^2 = 5.48$, $DF = 1$, $P = 0.02$; Fig. 5.4A). Small helpers had the lowest likelihood of showing submission towards the dominant breeders, and the likelihood of showing submission increased for medium helpers (mean \pm SE = 1.10 ± 0.57 , $Z = 1.95$, $DF = 1$, $P = 0.05$) and for large helpers (mean \pm SE = 2.06 ± 0.59 , $Z = 3.47$, $DF = 1$, $P < 0.001$). There was little evidence of an interaction between helper class and predation risk on the likelihood of showing submission to the dominants, as indicated by the low weight for the interaction model ($AIC_{\text{weight}} = 0.83$ vs 0.17 for non-interaction vs interaction model, respectively).

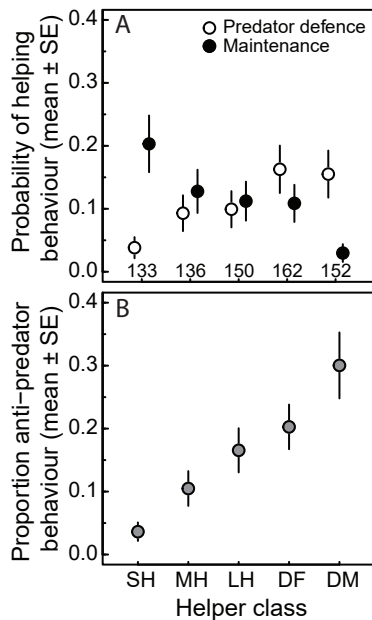


FIGURE 5.3 The mean probability (\pm SE) of (A) showing predator defence or maintenance behaviour for individuals of different status and size class (SH = small helper; MH = medium helper; LH = large helper, DF = dominant female, DM = dominant male). In (B) is shown the mean (\pm SE) relative proportion of anti-predator behaviours to all helping behaviours (i.e. maintenance and defence against all predators and space competitors). Numbers in (A) represent sample sizes for each class.

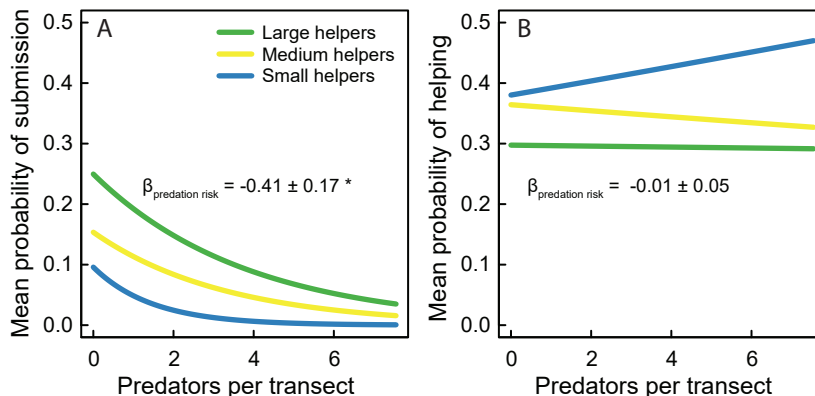


FIGURE 5.4 The mean probability of (A) submission towards the dominants and (B) providing help by different helper classes in relation to predation risk. Betas (β) represent overall conditional mean effect sizes (\pm SE) of predation risk on (A) the probability of submission and (B) the probability of helping. There were no significant interactions between helper class and predation risk for the probability of submission or helping (see results).

The likelihood of providing any kind of helping behaviour was independent of predation risk (mean \pm SE = 0.005 ± 0.05 , $\chi^2 = 0.02$, DF = 1, $P = 0.90$; Fig. 5.4B) and there were no indications that the likelihood of providing help differed between helper classes ($\chi^2 = 3.61$, DF = 1, $P = 0.17$) or that there was an interaction between predation risk and helper class (AICc_{weight} = 0.86 vs 0.14 for non-interaction and interaction model, respectively).

DISCUSSION

Social conflict can be a repellent force in the evolutionary transition to complex societies. Identifying the conditions that reduce social conflict are therefore important to understand why transitions occur in some species, but not in others (West *et al.* 2015). Our data show that dominants reduce aggression towards subordinates under increased risk of predation, presumably because subordinates provide fitness benefits under high predation risk. Similarly, conflict between subordinates in the same group decreased with increasing predation risk. In contrast, individuals did not reduce aggression towards close neighbours under increased predation risk, and reproductive success data indicated that the benefits of such neighbours are comparably small. Lower social conflict was not the result of subordinates increasing their helping effort, or submissive behaviours under increased predation risk.

Living with conspecifics can be beneficial, for example when this provides better access to food or protection against predators (Krause & Ruxton 2002). Such benefits can arise on multiple levels of social organisation – i.e. at the group and colony level (Jungwirth & Taborsky 2015). We show that that groups of *N. pulcher* benefit from the presence of helpers under increased risk of predation: small and large helpers increase the likelihood that a territory contains fry or juveniles, but only when predation risk was high (Fig. 5.1). Interestingly, there was no association between reproductive success and the number of medium-sized helpers. While smaller helpers invested most in the excavation of shelters (Fig. 5.3) that are important for other group members and provide safety for small fry (Balshine *et al.* 2001; Groenewoud *et al.* 2016), large helpers are important for defence against piscivorous predators, showing the highest levels of anti-predator defence (after the dominants; Fig. 5.3). Such defence has been shown to increase survival of other group members (Heg *et al.* 2004a). Increased group reproductive success and survival can be beneficial for all helper classes: related (mostly small) helpers can receive indirect benefits by raising kin and all group members can benefit from group augmentation effects (Kokko, Johnstone & Clutton-Brock 2001; Kingma *et al.* 2014) and improved group stability (Heg *et al.* 2005), which increases their chances of survival. Medium helpers were just as likely as large helpers to

show anti-predator defence, or maintenance behaviours (Fig. 5.3), but large helpers likely play a more important role in defence against larger predators. A post-hoc investigating of our data also indicates this: both medium and large helpers rarely defended against large predators, but medium helpers were more likely to attack small than medium predators (56% vs 38% of attacked predators), while large helpers were more likely to attack medium than small predators (71% vs 24% of attacked predators). Such differences might explain why large helpers, but not medium helpers have a positive effect on reproduction under elevated risk of predation.

Territory density had no consistent effect on the likelihood that territories contained fry or juveniles. While there was some indication of a three-way interaction between predation risk, the number of large helpers, and territory density on the likelihood of a territory containing fry, evidence for such this model (based on AICc weights) was rather low. This interaction could be expected based on previous findings, which suggests that small groups have highest reproductive success under high territory density, while large groups have higher reproductive success under low territory density (Jungwirth & Taborsky 2015). Such trade-offs are likely the result of either large groups, or many neighbours providing the optimal number and density of fish that participate in anti-predator defence (Jungwirth *et al.* 2015a; Groenewoud *et al.* 2016), but increased competition and lack of protection can be detrimental for large groups under high density, or small groups under low density, respectively. Predation risk is expected to shift this balance towards more defenders (i.e. group size *and* territory density) resulting in higher reproductive success. However, aggressive interactions between groups did not decrease with increasing predation risk (Fig. 5.2C). Previous studies on *N. pulcher* have found multiple benefits of having close neighbouring groups both for anti-predator defence and group persistence (Jungwirth & Taborsky 2015; Jungwirth *et al.* 2015a; Groenewoud *et al.* 2016), but effects on reproductive success were conditional on group size (Jungwirth & Taborsky 2015). Supposedly, the benefits of having neighbours under higher predation pressure does not provide sufficient additional benefits to select for reduced competition between neighbours. This might be because reduced competition (i) does not increase shared defence by neighbours, if such defence happens for purely selfish reasons (Jungwirth *et al.* 2015a) and/or (ii) any group that lowers investment in between-group competition loses resources to neighbouring groups.

Reduced conflict between individuals in groups is an important prerequisite in the transition to complex sociality (West *et al.* 2015). Previous findings in *N. pulcher* show that predation risk leads to reduced dispersal of large subordinates (Heg *et al.* 2004a) and higher acceptance of unrelated immigrants (Zöttl, Frommen & Taborsky 2013). Consequently, groups under high predation risk contain more large subordinates (Groenewoud *et al.* 2016). Our

data show that dominants are less likely to show aggression towards subordinates under elevated risk of predation, which likely facilitates such changes in dispersal and group composition and suggests that delayed dispersal by large subordinate might be (partly) driven by mutualistic benefits of cooperation (i.e. anti-predator defence) under increased threat of predation (Clutton-Brock 2002; Kingma *et al.* 2014). Reduced conflict between dominants and subordinates was not the result of increased levels of help or submissive behaviours that might appease dominants to show less aggression and which can be predicted by the pay-to-stay hypothesis (Gaston 1978; Quiñones *et al.* 2016). Our data is consistent with some reproductive skew models, which model within-group conflict and the partitioning of reproduction as a function of different social, genetic and ecological factors (Reeve, Emlen & Keller 1998; Kokko *et al.* 2001). In addition to enforcing help, dominant aggression can function to suppress or prevent competition for reproduction by larger subordinates (Dierkes, Taborsky & Kohler 1999; Heg, Bender & Hamilton 2004b; Fitzpatrick *et al.* 2005). Lowering levels of aggression would thus decrease the costs of group membership and relax the threshold at which subordinates would disperse, but increase the likelihood that large subordinate males engage in reproduction. One straightforward prediction from this line of reasoning would be that reproductive skew decreases (i.e. large subordinates obtain a larger share of reproduction) with increasing predation risk. Investigating conflict and levels of reproductive partitioning within groups in response to elevated predation risk could shed light on both the proximate and ultimate causes of sociality. We are currently not aware of any studies that have investigated the relationship between predation risk and reproductive skew, and of only one study that has shown reduced conflict and increased cooperation as a result of predation risk (Krams *et al.* 2010), or environmental harshness in general (Shen *et al.* 2012).

Aggression between subordinates in *N. pulcher* functions mainly to establish and maintain social hierarchies, and is mostly directed to group members that are close in rank (Wong & Balshine 2011). Levels of aggression are therefore expected to increase with the number of similar sized competitors and in fact our data shows that the likelihood of showing aggression increases with an increasing number of same size subordinates in the group. However, conflict is expected to be increasingly costly for individuals under increased predation risk because individuals invest less in helping behaviours which could negatively affect the fitness of other group members and group reproductive output. Furthermore, vigilance is lower during aggressive interactions, making individuals susceptible to predation (Jakobsson, Brick & Kullberg 1995; Hess, Fischer & Taborsky 2016). Accordingly, we show that subordinates reduce levels of within-group aggression towards each other with increasing predation risk. The consequences of reduced aggression and conflict for the resulting social hierarchy in *N. pulcher* is unknown, but it could mean that either hierarchies are established

using lower levels of aggression or that social hierarchies are less well established in groups under high risk of predation, which will have substantial implications for life history traits such as dispersal and growth (Heg *et al.* 2004b; Jordan, Wong & Balshine 2010).

Predation risk has been undervalued as a driver of complex sociality. Our study suggests that predation risk is an important ecological factor selecting for reduced levels of conflict within- but not between groups as a result of increased benefits of having subordinates under high predation risk. Reduced levels of conflict are important in the transition to complex sociality (West *et al.* 2015). This study corroborates and provides a potential mechanism for a previous finding, which show that groups under high predation risk have higher numbers of large helpers (Groenewoud *et al.* 2016). However, the benefits of having additional neighbours might be too small to offset competition for valuable resources between neighbouring groups, and consequently, our data shown no reduction of conflict between neighbouring groups as a result of increased predation risk. We argue that high relatedness, which is generally associated with the evolution of cooperation and sociality, is not a necessary condition for cooperation to evolve, but that ecological factors can select for cooperation when it provides mutual benefits.

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SUPPLEMENTARY INFORMATION

TABLE S5.1 Model comparisons for different helper size classes of models with varying relationships between reproductive success, predation risk, territory density and the number of helpers.

Large helpers							
Model structure	K	AICc	Δ AICc	AICc weight	Cumulative weight	Evidence ratio	Log-likelihood
PR x LH + TD	6	314.29	0	0.59	0.59		-150.97
PR x LH x TD	9	316.42	2.13	0.2	0.79	3	-148.82
PR + LH + TD	5	317.46	3.16	0.12	0.91	4.9	-153.6
PR x TD + LH	6	319.37	5.07	0.05	0.96	11.8	-153.5
PR + LH x TD	6	319.46	5.17	0.04	1	14.8	-153.55

PR = Predation risk, LH = number of large helpers, TD = territory density

Medium helpers							
Model structure	K	AICc	Δ AICc	AICc weight	Cumulative weight	Evidence ratio	Log-likelihood
PR + MH x TD	6	321.56	0	0.51	0.51		-154.6
PR + MH + TD	5	322.85	1.28	0.27	0.78	1.9	-156.3
PR x TD + MH	6	324.88	3.31	0.1	0.88	5.1	-156.26
PR x MH + TD	6	324.95	3.38	0.09	0.98	5.7	-156.3
PR x MH x TD	9	327.71	6.15	0.02	1	25.5	-154.47

PR = Predation risk, MH = number of medium helpers, TD = territory density

Small helpers							
Model structure	K	AICc	Δ AICc	AICc weight	Cumulative weight	Evidence ratio	Log-likelihood
PR x SH + TD	6	310.45	0	0.75	0.75		-149.05
PR + SH + TD	5	314.42	3.97	0.1	0.85	7.5	-152.08
PR x SH x TD	9	315.23	4.78	0.07	0.92	10.7	-148.23
PR + SH x TD	6	316.1	5.65	0.04	0.96	18.8	-151.87
PR x TD + SH	6	316.5	6.05	0.04	1	18.8	-152.07

PR = Predation risk, SH = number of small helpers, TD = territory density

TABLE S5.2 Model comparisons of social conflict (i.e. aggression) between dominants and subordinates, and between subordinates of the same social group.

Dominant to subordinate aggression

Model structure	K	AICc	Δ AICc	AICc weight	Cumulative weight	Evidence ratio	Log-likelihood
PR + GS + HC	7	310.52	0	0.48	0.48		-148.13
PR x HC + GS	9	312.12	1.6	0.22	0.7	2.18	-146.85
PR x GS + HC	8	312.51	1.99	0.18	0.88	2.67	-148.09
PR + GS x HC	9	313.54	3.02	0.11	0.99	4.36	-147.56
PR x GS x HC	14	317.78	7.26	0.01	1	48	-144.4

PR = Predation risk, GS = group size, HC = helper class (receiving)

Subordinate to subordinate aggression

Model structure	K	AICc	Δ AICc	AICc weight	Cumulative weight	Evidence ratio	Log-likelihood
PR + GS + HC	6	428.23	0	0.5	0.5		-208.01
PR x GS + HC	7	429.92	1.69	0.21	0.71	2.4	-207.82
PR + GS x HC	8	430.71	2.48	0.14	0.86	3.6	-207.18
PR x HC + GS	8	430.82	2.59	0.14	0.99	3.6	-207.23
PR x GS x HC	13	437	8.77	0.01	1	50	-205.05

PR = Predation risk, GS = group size, HC = helper class

