

Benefits of coloniality: communal defence saves anti-predator effort in cooperative breeders

Arne Jungwirth*, Dario Josi, Jonas Walker and Michael Taborsky

Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, 3032 Hinterkappelen, Switzerland

Summary

1. Many anti-predator benefits of group living are predicted to scale with prey density. Nevertheless, evidence for a general density-dependent increase of prey survival is scarce. A possible reason for this discrepancy is the reduction of costly anti-predator behaviour of prey with increasing density, which may offset density-dependent survival gains. Benefits of group living might hence accrue by saved investment into anti-predator behaviours rather than by increased survival rates.

2. Here, we experimentally presented predators in a colony of the cooperatively breeding cichlid fish *Neolamprologus pulcher* to study density dependence of their anti-predator defences. Predation is a driver of the formation and stability of breeding groups in this species, but potential benefits of coloniality are yet unclear. We hypothesised that increased density of breeding groups would either increase total anti-predator behaviour or allow individuals to reduce their anti-predator effort due to enhanced predator deterrence from neighbours.

3. Confirming predictions from the second hypothesis, our results show that focal groups invested less into anti-predator behaviour at higher densities, while neighbouring groups' behaviour compensated for this reduced effort. This resulted in stable levels of anti-predator behaviours over the entire range of natural densities. Thus, aggregating in colonies allows these fish to save investment in anti-predator behaviour.

4. These results suggest that the formation of both breeding groups and colonies reflects adaptive responses to high predation pressure in this species. Two different levels of sociality seem to be favoured by the same selective force.

5. Our study provides experimental evidence in nature for an important benefit of coloniality that may explain the concomitant existence of different levels of sociality in many highly social taxa.

Key-words: anti-predator effort, colony, communal defence, density, group living, predation

Introduction

A major ecological cause of group living is the prevalence of high predation pressure (Rubenstein 1978; Krause & Ruxton 2002). When animals aggregate, *per capita* predation risk typically decreases due to dilution or similar effects that scale with density (Wrona & Dixon 1991; Bednekoff & Lima 1998; Beauchamp 2014). In addition, the anti-predator defences of potential prey may reduce predation risk through grouping due to greater efficacy and/or reduced costs (Krause & Ruxton 2002). In fact, in a range of systems, denser or larger aggregations have been shown to (i) yield survival benefits to individuals, (ii) to increase

total anti-predator behaviour, and (iii) to reduce the costs of anti-predator behaviours (Hoogland & Sherman 1976; Hoogland 1981; Dominey 1983; Brown & Brown 1987, 2004; Wiklund & Andersson 1994; Arroyo, Mougeot & Bretagnolle 2001; Serrano *et al.* 2005; Krams *et al.* 2007). Nevertheless, a lack of density-dependent anti-predator benefits has also been reported from several species (Rodgers Jr 1987; Bellinato & Bogliani 1995; Brunton 1997; Stokes & Boersma 2000). Based on these contradicting findings, the general role of anti-predator benefits for the evolution of large animal aggregations has been questioned (Clode 1993; Danchin & Wagner 1997; Rolland, Danchin & de Fraipont 1998; Wagner *et al.* 2000; Varela, Danchin & Wagner 2007). One potential explanation for these ambivalent findings is the adjustment of anti-predator

*Correspondence author. E-mail: arne.jungwirth@gmx.net

behaviours of prey to their respective density (Daly *et al.* 2012). If individuals are either indifferent in their anti-predator behaviour with regard to density, or if they increase their investment at higher densities because attacks on predators are less risky, for instance due to dilution effects, higher densities of prey may result in increased total anti-predator effort (Brown & Hoogland 1986; Arroyo, Mougeot & Bretagnolle 2001; Ostreier 2003). Alternatively, higher densities of prey can cause individuals to reduce their defence effort, as the combined effort of other individuals may compensate for this reduction; in this case, similar *per capita* predation risk may ensue across a wide range of prey densities (Daly *et al.* 2012; Schädelin, Fischer & Wagner 2012). In case such compensatory effects do not apply, higher prey densities might even result in increased predation risk, for instance because of an unproportionally large reduction of total anti-predator behaviour of individuals or due to an increased attractiveness of higher prey densities to predators. In this case, aggregating would only be adaptive if it yielded benefits other than reduced predation (Bellinato & Bogliani 1995; Davis & Brown 1999; Stokes & Boersma 2000). Consequently, anti-predator benefits of group living may not be detected by density-dependent variation in predation rates, but rather by the anti-predator effort expended by individuals (Daly *et al.* 2012).

When prey reduce their anti-predator behaviours with increasing density, this may either cause density-dependent benefits of group-living to all individuals in the population by their saving expenses (e.g. risk or time; cf. Roberts 1996), even if their predation risk is not reduced (Daly *et al.* 2012), or it may asymmetrically inflict costs on others, if individuals reducing anti-predator behaviours such as mobbing (Poiani & Yorke 1989), alarm calling (Zuberbühler 2009), defence (Daly *et al.* 2012), vigilance (Fortin *et al.* 2004), or predator inspection (Milinski *et al.* 1997) freeride on the efforts of their peers (Rankin, Bargum & Kokko 2007). In this context, the crucial question is how costly anti-predator behaviours that primarily benefit others can be evolutionarily stable (Maynard Smith 1965; Bergstrom & Lachmann 2001; Garay 2009; Archetti 2011; Sirot 2012). Similar social dilemmas are ubiquitous in shared investments. When individuals expend time and energy or assume a risk to the benefit of a group, this creates incentives for individual group members to save own investment while free riding on the investment of others (e.g. Johnstone *et al.* 2014). If group living is a selected response to predation, the quantity of total and individual anti-predator behaviour shown in dependence of prey density will indicate whether group members mutually benefit from each other's effort, or whether they are subject to such a social dilemma.

It is currently unclear to which extent different levels of social organization such as breeding groups and colonies can mutually contribute to anti-predator benefits of individuals, because most research has focused on only one level of social organization, that is either groups or colonies (Rubenstein 1978; Griesser, Nystrand & Ekman 2006;

Varela, Danchin & Wagner 2007; Heg & Taborsky 2010; Krams *et al.* 2010).

Here, we test the hypothesis that the observed aggregation of groups of the cooperatively breeding cichlid fish *Neolamprologus pulcher* into colonies, that is assemblages of a few up to some hundred groups in close proximity, yields anti-predator benefits (Heg *et al.* 2008). In particular, we ask whether defence effort against predators depends on (i) the density of groups and (ii) the behaviour of neighbouring groups. In this species, reproductive groups composed of individuals varying in age and size defend territories in which group members find breeding substrate and shelter from predators (Taborsky & Limberger 1981; Balshine *et al.* 2001). Large group members actively protect smaller ones by attacking predators, and this protection is crucial for juvenile survival (Taborsky 1984; Heg *et al.* 2004; Brouwer, Heg & Taborsky 2005). Hence, the formation of cooperatively breeding groups appears to be largely driven by predation. The benefits of the aggregation of groups into colonies are hitherto less clear, as predator densities within a colony are similar or even higher than at comparable sites outside of colonies (Heg *et al.* 2008). Nevertheless, individuals show a clear preference to occupy vacancies within rather than outside colonies (Heg *et al.* 2008). The aim of this study was to test experimentally whether individuals benefit from coloniality either by an increase in total anti-predator behaviour or by individually saving anti-predator effort (cf. Clarke & Fitzgerald 1994). To check whether group members adjust their defence behaviour to local group density, we recorded the anti-predator effort shown by groups located in areas of different densities within the same colony. We expected predators either to receive more aggression in denser areas due to the combined effort of several groups, or to receive similar or lower aggression levels if groups located in denser areas would show reduced anti-predator investment. We further investigated whether the defence effort shown by focal groups is adjusted to the defence effort of neighbouring groups. The results of our experimental predator presentations should hence clarify whether there are anti-predator benefits of coloniality in these cooperative breeders and, if so, whether such benefits arise from an increase in total anti-predator activities in areas of high group density, or from saved anti-predator effort of group members.

Materials and methods

We studied a natural population of *N. pulcher*, a cichlid fish distributed along the rocky shores of Lake Tanganyika, East Africa (Duftner *et al.* 2007). In *N. pulcher*, (i) group members cooperatively defend territories with shelters for hiding and breeding (Taborsky & Limberger 1981; Balshine *et al.* 2001); (ii) larger group members provide protection crucial for juvenile survival (Taborsky 1984; Heg *et al.* 2004; Brouwer, Heg & Taborsky 2005), and (iii) groups cluster together, forming colonies (Heg *et al.* 2005, 2008; Stiver *et al.* 2007). To study a colony of these fish, we used scuba-diving at 10–12 m depth at Kasakalawe Point, west of Mpulungu, Zambia (8°46'849'S, 31°04'882'E). Here, the main

predator of adult and subadult *N. pulcher* [i.e. >1.5 cm standard length (SL)] is the piscivorous cichlid *Lepidolamprologus elongatus* (Balshine et al. 2001; Heg et al. 2004).

To assess how local densities of *N. pulcher* groups influence anti-predator behaviour, we presented focal groups with simulated predator attacks. A total of 73 groups were haphazardly selected in a way to cover the entire density variation observed in the study area (a colony stretching approximately 30 × 30 m, with 166 groups in total; Fig. 1). Each focal group experienced two consecutive presentations of 2 min each that were preceded by a habituation phase of 3 min. During each presentation, a clear plexiglass tube (14 cm length, 9 cm diameter, closed with perforated lids to allow water exchange) containing a live *L. elongatus* was placed at one of two positions on the focal territory's border (cf. Fig. 1): either in the direction of the nearest neighbouring *N. pulcher* territory (towards nearest neighbour: TNN) or in the direction of the least densely settled area bordering the focal territory (away from neighbours: AFN). The sequence of presentations was randomized between focal groups. Pilot experiments had shown that groups of *N. pulcher* only reacted to the stimulus fish when it was presented in their immediate vicinity. Thus, regarding the focal group's behaviour, the predator was as likely to be attacked in the TNN as in the AFN position. For neighbouring groups, however, the predator was unlikely to be attacked in the AFN position, and its probability of being attacked in the TNN position depended on the nearest neighbouring group's distance to the respective focal group. This allowed us to disentangle the focal group's response to their nearest neighbouring group's acute anti-predator behaviour (the difference in the focal group's investment between the TNN and AFN positions) from a general behavioural adjustment to density (by comparing the investment of focal groups between different densities). To serve as stimulus fish, 22 *L. elongatus* were caught within 10 m of *N. pulcher* territories in the study area (median SL: 10.1 cm; range: 8.3–13.3 cm; pilot experiments revealed that *N. pulcher* reacted strongest to *L. elongatus* of this size range).

For all focal groups, we determined the distance (in metres from centre to centre, ±0.05 m) to the nearest neighbouring foreign territory. We also counted the number of foreign territories within a 2-m radius around each focal territory. These measures were highly correlated (Spearman's rank correlation: $n = 73$, $\rho = -0.69$, $P < 0.001$), so we used nearest neighbour distance as an index of local population density. We counted all fish larger than 3.5 cm SL (i.e. dominant males, dominant females and potentially mature helpers; cf. Heg et al. 2004) for each group. We did not include smaller individuals in the count, as these typically

do not engage in territory defence against large piscivores (Heg & Taborsky 2010; A. Jungwirth, personal observation).

During each presentation, we recorded the number of aggressive behaviours directed towards the stimulus fish by the members of the focal group and of the nearest neighbouring group. We scored each attempt to ram or bite the predator and all frontal displays towards the predator (cf. Taborsky & Grantner 1998). To control for effects of group size, we divided the number of recorded aggressive behaviours by the number of large individuals (i.e. >3.5 cm, see above) in the respective territories.

Neither the recorded behaviours, nor group sizes, nor nearest neighbour distances were normally distributed. Thus, we applied generalized linear models (GLM) and nonparametric, two-tailed statistical tests (Wilcoxon matched-pairs signed-ranks test; Spearman's rank correlation test), using R version 3.0.2 (R Development Core Team 2013). When analysing counts of aggressive behaviours directed towards the stimulus fish, GLMs were fitted with a logarithmic link function to account for a Poisson error structure (family: poisson or quasipoisson; GLM log link). When analysing how the total anti-predator effort was shared between the focal group and the neighbouring group, GLMs were fitted with a logistic link function to account for a binomial error structure (family: quasibinomial; GLM logit link). GLMs did not include any terms other than the response variable of interest (counts of aggression of focal groups, neighbouring groups, or both, and relative share in anti-predator effort, respectively) and the explanatory variable of interest (nearest neighbour distance of the territory, or size of the group, respectively).

All work reported here conformed with the legal requirements of Zambia and was acknowledged by the Department of Fisheries in Mpulungu, Zambia.

Results

The median nearest neighbour distance of our experimental territories was 0.58 m (range: 0.16–3.2 m, $n = 73$), which well represented the distribution of nearest neighbour distances in the whole colony (median: 0.6 m, range: 0.16–3.2 m, $n = 166$).

The position at which the stimulus fish was presented (TNN or AFN, see Materials and methods) neither influenced the total amount of aggression performed against the predator (i.e. the sum of aggressive behaviours directed towards the stimulus fish by the members of the focal

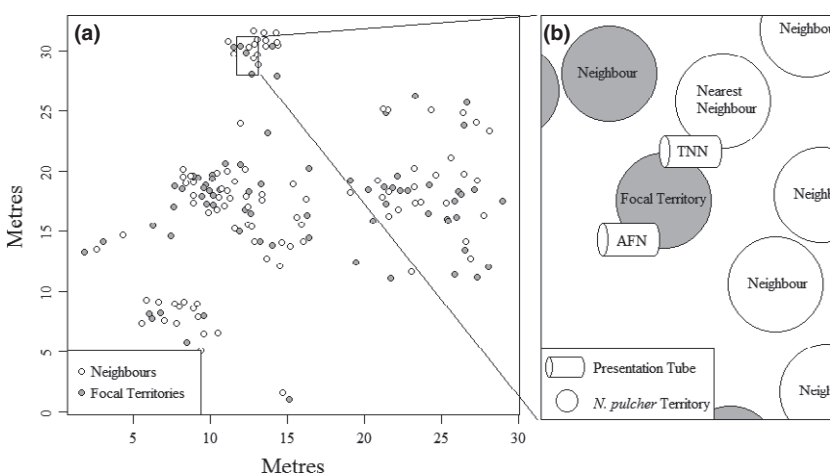


Fig. 1. Schematic territory map of the study area (a) and experimental set-up (b). The 73 focal territories haphazardly selected for the experiment are marked in grey. Each focal group was challenged with two simulated intrusions of a *Lepidolamprologus elongatus* presented at the territory border. Intrusions occurred either towards the nearest neighbouring territory (TNN) or towards the least densely populated area bordering the focal territory (AFN).

group and of its nearest neighbouring group; Wilcoxon matched-pairs signed-ranks test (hereafter: Wilcoxon test): $n = 73$, $V = 1439.5$, $P = 0.25$), nor the focal group's amount of aggression shown towards the predator (Wilcoxon test: $n = 73$, $V = 935.5$, $P = 0.33$). Neighbouring *N. pulcher* attacked the stimulus fish significantly more often when it was presented at the TNN compared to the AFN position (Wilcoxon test: $n = 73$, $V = 725$, $P < 0.001$; Fig. 2).

A given focal group's aggression towards the predator was strongly correlated between the presentations at the TNN and AFN positions (Spearman's rank correlation test: $n = 73$, $\rho = 0.571$, $P < 0.001$). During presentations at the TNN positions, there was no relationship between a focal group's and its nearest neighbouring group's aggression (Spearman's rank correlation test: $n = 73$, $\rho = -0.028$, $P = 0.82$). Larger focal groups showed more aggression (summed for both presentations) towards the predator (GLM log link: $n = 73$, $z = 5.13$, $P < 0.001$), while larger neighbouring groups attacked the predator less often (GLM log link: $n = 73$, $z = -3.87$, $P < 0.001$). When

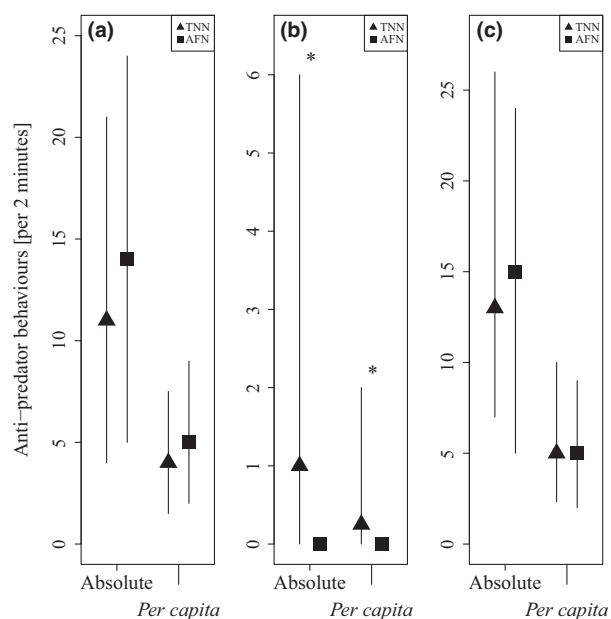


Fig. 2. The amount of anti-predator behaviour shown by large group members (cf. Materials and methods) towards the predator during each 2-min presentation. The predator was presented on the border of the focal territory, either towards the nearest neighbouring territory (towards nearest neighbour: TNN; triangles) or towards the least densely populated adjacent area (away from neighbours: AFN; squares). Data are presented for (a) focal groups, (b) nearest neighbouring groups and (c) the sum of all anti-predator behaviours (i.e. all anti-predator behaviours performed by the focal group and their nearest neighbouring group). Each symbol represents the median, and each line spans the upper and lower quartiles across all experimental trials. The two left columns in each plot depict absolute counts of aggressive behaviours, and the two right boxes in each plot depict values corrected for group size (i.e. counts of aggression divided by the number of large individuals). Mind the different scaling of the ordinate. Significant differences (cf. Results) are indicated by asterisks.

combining group sizes of focal groups and of their nearest neighbours to investigate whether anti-predator effort was affected by the total number of participating individuals, the exposed predator received similar amounts of aggression, irrespective of the number of large individuals present in both groups (GLM log link: $n = 73$, $z = -0.98$, $P = 0.33$). *Per capita* aggression (aggression during both presentations divided by group size) tended to be lower in larger focal groups (GLM log link: $n = 73$, $t = -1.82$, $P = 0.074$) and in larger neighbouring groups (GLM log link: $n = 73$, $t = -1.82$, $P = 0.073$), and this effect was statistically significant when combining focal and neighbouring groups (GLM log link: $n = 73$, $t = -2.84$, $P = 0.006$).

Correcting for group size, we found that with decreasing density of groups, the aggression of focal group members towards the predator increased (GLM log link: $n = 73$, $z = 2.18$, $z = -7.1$, $P = 0.029$; Fig. 3), while that of neighbouring group members declined (GLM log link: $n = 73$, $P < 0.001$; Fig. 3). In consequence, the total amount of aggression directed towards the predator did not change systematically with varying local densities (GLM log link: $n = 73$, $z = -0.55$, $P = 0.59$; Fig. 3).

The same effects were observed when no correction for group size was applied and absolute numbers of aggressive acts were used in the analyses: focal groups increased their anti-predator effort with decreasing density of groups (GLM log link: $n = 73$, $z = 5.28$, $P < 0.001$), neighbouring groups decreased their aggression with decreasing density (GLM log link: $n = 73$, $z = -11.43$, $P < 0.001$), and the

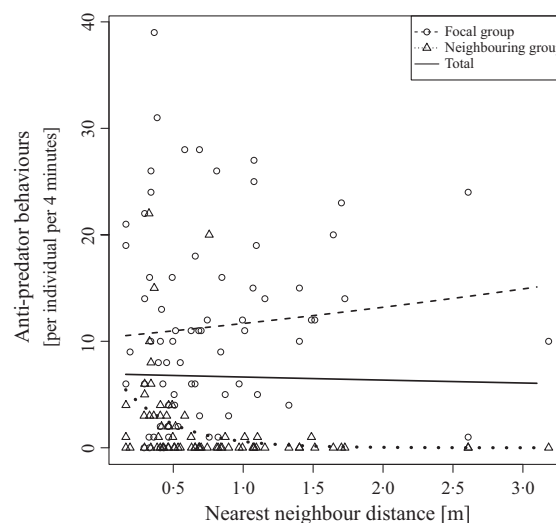


Fig. 3. The amount of *per capita* anti-predator behaviour shown towards the *Lepidolamprologus elongatus* at each focal territory during 4 min of experimental presentation (2 + 2 min, both presentations combined) as a function of the density (represented by the nearest neighbour distance of the focal territory). Behaviours of focal groups are represented by circles, those of neighbouring groups by triangles. Trend lines are based on values predicted by the GLMs used for analysis (cf. Results; dashed line: focal groups; dotted line: neighbouring groups; solid line: total *per capita* anti-predator effort).

total amount of aggression directed towards the predator remained similar across all densities (GLM log link: $n = 73$, $z = 0.88$, $P = 0.38$).

With increasing density, focal groups provided a significantly larger share of the total aggression directed towards the predator (GLM logit link: $n = 73$, $t = 3.38$, $P = 0.001$). This effect was even clearer when only considering aggression during the TNN presentation (GLM logit link: $n = 73$, $t = 4$, $P < 0.001$; Fig. 4). We did not detect any influence of focal group size on a focal group's share in anti-predator effort (GLM logit link: $n = 73$, $t = 0.99$, $P = 0.33$), nor did the difference between the focal group's size and the neighbouring group's size influence their share in anti-predator effort (GLM logit link: $n = 73$, $t = 1.15$, $P = 0.26$).

Discussion

Groups of *N. pulcher* adjust their anti-predator behaviour to local population density: the higher the local density, the less anti-predator behaviour was shown by members of focal groups *per capita* and by the groups as a whole (Fig. 3). This indicates that groups of *N. pulcher* benefit from aggregating in colonies, as it allows them to reduce their anti-predator effort. The reduced anti-predator effort by focal groups was compensated by increased efforts of their nearest neighbours at higher densities, resulting in similar levels of aggression directed towards the predator, irrespective of local density in the colony (Fig. 2). This suggests that the potential social dilemma

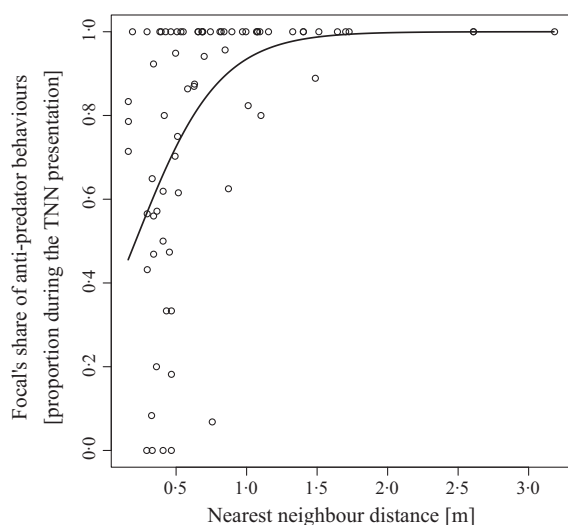


Fig. 4. Each focal group's relative share of total anti-predator investment during the TNN presentation as a function of its nearest neighbour distance. Each dot represents a single presentation at a unique focal territory. Values of 1 indicate that the focal group provided all anti-predator effort; values of 0 indicate that the neighbouring group provided all anti-predator effort. The trend line is based on values predicted by the respective GLM (cf. Results). Points were jittered around their x value to increase visibility.

inherent in joint anti-predator activities of aggregations does not cause free riding between groups of *N. pulcher*. Groups neither took turns in attacking the predator, nor did we observe any other form of coordination (cf. Hoogland & Sherman 1976; Krams *et al.* 2007; Johnstone *et al.* 2014). In fact, we did not detect any correlation between a neighbouring group's immediate effort and the respective focal group's anti-predator investment. Furthermore, focal groups did not differentiate between the two presentation sites (TNN and AFN; cf. Figs 1 and 2), even though neighbours only attacked the predator when it was presented close to their own territory (TNN). Nevertheless, focal groups received less support from neighbours and provided a larger share of the total anti-predator effort the further away the respective neighbouring group was located (cf. Fig. 4). Thus, we assume that *N. pulcher* follow a simple rule of thumb, whereby they adjust anti-predator defence in response to the presence or absence of close neighbours (cf. Lima 1995; Welton, McNamara & Houston 2003). They do so irrespective of others' immediate effort and only when the predator poses a direct threat to their own group, but in a way that reflects the likelihood of receiving support in anti-predator behaviour.

Together, the effects of reduced individual investment in anti-predator behaviour and compensation by neighbours will likely benefit groups located at denser parts of a colony. It is important to note that direct assessment of predation risk and predator deterrence efficiency is beyond the scope of this study (cf. Brown & Hoogland 1986; Curio & Regelman 1986; Martin & Taborsky 1997). Predation events are rarely observed, and thus predation rates are difficult to estimate (cf. Balshine *et al.* 2001). Nevertheless, larger groups have been shown to survive longer, which indicates density-dependent predation risk at the group level (Heg *et al.* 2005). It seems likely that similar effects also occur at the colony level, favouring groups with many adjacent neighbours. Indeed, our long-term data on group size and group survival in the study area show that larger groups are found in denser areas and that both high density and large group size favour group survival (own unpublished data; see also Heg *et al.* 2005). Consequently, it seems likely that positive anti-predator effects similar to those observed at the group level (Heg *et al.* 2004) also occur at the colony level, favouring groups with many adjacent neighbours. Thus, two different levels of social organization, cooperative breeding and coloniality, both seem to reflect adaptations to the same cause: high predation pressure.

Our results differ somewhat from those found in a laboratory study of the colonial, biparental congener *Neolampyris caudapunctatus* (Schädlein, Fischer & Wagner 2012), where newly introduced pairs reduced their anti-predator behaviour and free rode on the effort of already established neighbours. This also led to stable levels of anti-predator effort at the focal pair's territory, but the investment of the two parties was asymmetric, with one

party clearly exploiting the effort of the other. A recent laboratory study using *N. pulcher* showed that dominant individuals' anti-predator effort was unaffected by the presence of neighbours, but subordinates changed their investment in response to a neighbour's presence and familiarity (Hellmann & Hamilton 2014). In contrast to our results, subordinates in that study increased their anti-predator behaviour in the presence of neighbours, especially when these were unfamiliar. The key findings of these two studies are not easily comparable with our work. The experimental asymmetry between pairs in the laboratory study of Schädelin, Fischer & Wagner (2012) differs from our groups in the field, where both focal and neighbouring groups had defended their territories for at least 2 months prior to the experiments (and probably much longer). Similarly, the conditions in Hellman & Hamilton's laboratory study (2014) differed significantly from our field experiment: their groups had no physical contact with each other and lived in an otherwise predator-free environment. Also, Hellmann and Hamilton used a different type of predator that only posed a threat to the fry of *N. pulcher*, whereas our stimulus fish were potentially threatening to a much larger range of group members (Heg *et al.* 2004; Heg & Taborsky 2010). The divergence of these results suggests that between-group interactions in anti-predator behaviour might be strongly context-dependent. Notably, asymmetries between the interacting parties, their familiarity with each other, the type of predator used, and the potential for interactions between the parties seem to influence anti-predator behaviour in different ways. Thus, there might be no general framework clearly predicting how anti-predator behaviour will change, without explicitly incorporating these and probably even more factors. Furthermore, while laboratory studies allow for fine-tuned experimental approaches to study detailed behavioural questions, their predictive value for an understanding of broad-scale anti-predator behaviour in natural systems might be limited.

In conclusion, our results demonstrate anti-predator benefits of coloniality in a wild vertebrate, which adds to the survival benefits of group living in this species (Taborsky 1984; Heg *et al.* 2004). Similar effects might apply in other cooperative breeders where breeding groups aggregate [e.g. bell miners (Painter *et al.* 2000); prairie dogs (Hoogland 1983)], as well as in other colonial species in which individuals communally defend against predators, but where benefits of coloniality remain elusive [e.g. least terns (Brunton 1997); purple martins (Davis & Brown 1999)]. Importantly, the benefits of coloniality were not detected in total anti-predator behaviour, but at the level of individuals and groups. Thus, individual reduction in anti-predator behaviour to save effort and/or mutual compensation may generally mask survival benefits generated by coloniality (Daly *et al.* 2012). Our study demonstrates that one important benefit of coloniality may be the reduction of anti-predator effort. This may benefit individuals by saving time, energy, and risk while not compromising

survival due to the combined anti-predator measures of different groups.

Acknowledgements

We thank Danny Sinyinza and the staff at the Department of Fisheries in Mpulungu, Zambia, for logistic support. We are grateful to Celestine Mwewa and the staff at the Tanganyika Science Lodge for their hospitality. Ian Hamilton and two anonymous reviewers provided comments that greatly improved the manuscript. Funding was provided via SNF Grant No 310030B 138660 to MT.

Data accessibility

Data are available in the Dryad repository <http://dx.doi.org/10.5061/dryad.88qt1> (Jungwirth *et al.* 2015).

References

- Archetti, M. (2011) A strategy to increase cooperation in the volunteer's dilemma: reducing vigilance improves alarm calls. *Evolution*, **65**, 885–892.
- Arroyo, B., Mougeot, F. & Bretagnolle, V. (2001) Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). *Behavioral Ecology and Sociobiology*, **50**, 109–115.
- Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M. & Werner, N.Y. (2001) Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). *Behavioral Ecology and Sociobiology*, **50**, 134–140.
- Beauchamp, G. (2014) *Social Predation: How Group Living Benefits Predators and Prey*. Academic Press, London, UK.
- Bednekoff, P.A. & Lima, S.L. (1998) Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proceedings of the Royal Society B: Biological Sciences*, **265**, 2021–2026.
- Bellinato, F. & Bogliani, G. (1995) Colonial breeding imposes increased predation: experimental studies with herons. *Ethology Ecology & Evolution*, **7**, 347–353.
- Bergstrom, C.T. & Lachmann, M. (2001) Alarm calls as costly signals of antipredator vigilance: the watchful babbler game. *Animal Behaviour*, **61**, 535–543.
- Brouwer, L., Heg, D. & Taborsky, M. (2005) Experimental evidence for helper effects in a cooperatively breeding cichlid. *Behavioral Ecology*, **16**, 667–673.
- Brown, C.R. & Brown, M.B. (1987) Group-living in cliff swallows as an advantage in avoiding predators. *Behavioral Ecology and Sociobiology*, **21**, 97–107.
- Brown, C.R. & Brown, M.B. (2004) Group size and ectoparasitism affect daily survival probability in a colonial bird. *Behavioral Ecology and Sociobiology*, **56**, 498–511.
- Brown, C.R. & Hoogland, J.L. (1986) Risk in mobbing for solitary and colonial swallows. *Animal Behaviour*, **34**, 1319–1323.
- Brunton, D.H. (1997) Impacts of predators: center nests are less successful than edge nests in a large nesting colony of least terns. *The Condor*, **99**, 372–380.
- Clarke, M.F. & Fitzgerald, G.F. (1994) Spatial-organization of the cooperatively breeding bell miner *Manorina melanophrys*. *Emu*, **94**, 96–105.
- Clode, D. (1993) Colonially breeding seabirds: predators or prey? *Trends in Ecology & Evolution*, **8**, 336–338.
- Curio, E. & Regelmann, K. (1986) Predator harassment implies a real deadly risk: a reply to Hennessy. *Ethology*, **72**, 75–78.
- Daly, D., Higginson, A.D., Chen, D., Ruxton, G.D. & Speed, M.P. (2012) Density-dependent investment in costly anti-predator defences: an explanation for the weak survival benefit of group living. *Ecology Letters*, **15**, 576–583.
- Danchin, E. & Wagner, R.H. (1997) The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution*, **12**, 342–347.
- Davis, J.A. & Brown, C.R. (1999) Costs of coloniality and the effect of colony size on reproductive success in purple martins. *The Condor*, **101**, 737–745.
- Dominey, W. (1983) Mobbing in colonially nesting fishes, especially the bluegill, *Lepomis macrochirus*. *Copeia*, **1983**, 1086–1088.

- Duftner, N., Sefc, K.M., Koblmüller, S., Salzburger, W., Taborsky, M. & Sturmbauer, C. (2007) Parallel evolution of facial stripe patterns in the *Neolamprologus brichardi/pulcher* species complex endemic to Lake Tanganyika. *Molecular Phylogenetics and Evolution*, **45**, 706–715.
- Fortin, D., Boyce, M.S., Merrill, E.H., Fryxell, J.M. & Foraging, J.M. (2004) Foraging costs of vigilance in large mammalian herbivores. *Oikos*, **107**, 172–180.
- Garay, J. (2009) Cooperation in defence against a predator. *Journal of Theoretical Biology*, **257**, 45–51.
- Griesser, M., Nystrand, M. & Ekman, J. (2006) Reduced mortality selects for family cohesion in a social species. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1881–1886.
- Heg, D. & Taborsky, M. (2010) Helper response to experimentally manipulated predation risk in the cooperatively breeding cichlid *Neolamprologus pulcher*. *PLoS One*, **5**, e10784.
- Heg, D., Bachar, Z., Brouwer, L. & Taborsky, M. (2004) Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 2367–2374.
- Heg, D., Brouwer, L., Bachar, Z. & Taborsky, M. (2005) Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*, **142**, 1615–1641.
- Heg, D., Heg-Bachar, Z., Brouwer, L. & Taborsky, M. (2008) Experimentally induced helper dispersal in colonially breeding cooperative cichlids. *Environmental Biology of Fishes*, **83**, 191–206.
- Hellmann, J.K. & Hamilton, I.M. (2014) The presence of neighbors influences defense against predators in a cooperatively breeding cichlid. *Behavioral Ecology*, **25**, 386–391.
- Hoogland, J.L. (1981) The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology*, **62**, 252–272.
- Hoogland, J.L. (1983) Black-tailed prairie dog colonies are cooperatively breeding units. *The American Naturalist*, **121**, 275–280.
- Hoogland, J.L. & Sherman, P.W. (1976) Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecological Monographs*, **46**, 33–58.
- Johnstone, R.A., Manica, A., Fayet, A.L., Caswell Stoddard, M., Rodriguez-Girones, M.A. & Hinde, C.A. (2014) Reciprocity and conditional cooperation between great tit parents. *Behavioral Ecology*, **25**, 216–222.
- Jungwirth, A., Josi, D., Walker, J. & Taborsky, M. (2015) Data from: Benefits of coloniality: communal defence saves anti-predator effort in cooperative breeders. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.88qt1>
- Krams, I., Krama, T., Igaune, K. & Mänd, R. (2007) Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*, **62**, 599–605.
- Krams, I., Bērziņš, A., Krama, T., Wheatcroft, D., Igaune, K. & Rantala, M.J. (2010) The increased risk of predation enhances cooperation. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 513–518.
- Krause, J. & Ruxton, G.D. (2002) *Living in Groups*. Oxford University Press, Oxford, UK.
- Lima, S.L. (1995) Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, **49**, 11–20.
- Martin, E. & Taborsky, M. (1997) Alternative male mating tactics in a cichlid, *Pelvicachromis pulcher*: a comparison of reproductive effort and success. *Behavioral Ecology and Sociobiology*, **41**, 311–319.
- Maynard Smith, J. (1965) The evolution of alarm calls. *The American Naturalist*, **99**, 59–63.
- Milinski, M., Lüthi, J.H., Eggler, R. & Parker, G.A. (1997) Cooperation under predation risk: experiments on costs and benefits. *Proceedings of the Royal Society B: Biological Sciences*, **264**, 831–837.
- Ostreiher, R. (2003) Is mobbing altruistic or selfish behaviour? *Animal Behaviour*, **66**, 145–149.
- Painter, J.N., Crozier, R.H., Poiani, A., Robertson, R.J. & Clarke, M.F. (2000) Complex social organization reflects genetic structure and relatedness in the cooperatively breeding bell miner, *Manorina melanophrys*. *Molecular Ecology*, **9**, 1339–1347.
- Poiani, A. & Yorke, M. (1989) Predator harassment: more evidence on the deadly risk. *Ethology*, **83**, 167–169.
- R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rankin, D.J., Bargum, K. & Kokko, H. (2007) The tragedy of the commons in evolutionary biology. *Trends in Ecology & Evolution*, **22**, 643–651.
- Roberts, G. (1996) Why individual vigilance declines as group size increases. *Animal Behaviour*, **51**, 1077–1086.
- Rodgers, J.A. Jr (1987) On the antipredator advantages of coloniality: a word of caution. *The Wilson Bulletin*, **99**, 269–271.
- Rolland, C., Danchin, E. & de Fraipont, M. (1998) The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. *The American Naturalist*, **151**, 514–529.
- Rubenstein, D.I. (1978) On predation, competition, and the advantages of group living. *Perspectives in Ethology*, **3**, 205–231.
- Schädelin, F.C., Fischer, S. & Wagner, R.H. (2012) Reduction in predator defense in the presence of neighbors in a colonial fish. *PLoS One*, **7**, e35833.
- Serrano, D., Oro, D., Ursua, E. & Tella, J.L. (2005) Colony size selection determines adult survival and dispersal preferences: allee effects in a colonial bird. *The American Naturalist*, **166**, E22–E31.
- Siro, E. (2012) Negotiation may lead selfish individuals to cooperate: the example of the collective vigilance game. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2862–2867.
- Stiver, K., Desjardins, J., Fitzpatrick, J., Neff, B., Quinn, J.S. & Balshine, S. (2007) Evidence for size and sex-specific dispersal in a cooperatively breeding cichlid fish. *Molecular Ecology*, **16**, 2974–2984.
- Stokes, D.L. & Boersma, P.D. (2000) Nesting density and reproductive success in a colonial seabird, the *Magellanic penguin*. *Ecology*, **81**, 2878–2891.
- Taborsky, M. (1984) Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Animal Behaviour*, **32**, 1236–1252.
- Taborsky, M. & Grantner, A. (1998) Behavioural time-energy budgets of cooperatively breeding *Neolamprologus pulcher* (Pisces: Cichlidae). *Animal Behaviour*, **56**, 1375–1382.
- Taborsky, M. & Limberger, D. (1981) Helpers in fish. *Behavioral Ecology and Sociobiology*, **8**, 143–145.
- Varela, S.A.M., Danchin, E. & Wagner, R.H. (2007) Does predation select for or against avian coloniality? A comparative analysis. *Journal of Evolutionary Biology*, **20**, 1490–1503.
- Wagner, R.H., Danchin, E., Boulinier, T. & Helfenstein, F. (2000) Colonies as byproducts of commodity selection. *Behavioral Ecology*, **11**, 572–573.
- Welton, N.J., McNamara, J.M. & Houston, A.I. (2003) Assessing predation risk: optimal behaviour and rules of thumb. *Theoretical Population Biology*, **64**, 417–430.
- Wiklund, C.G. & Andersson, M. (1994) Natural selection of colony size in a passerine bird. *Journal of Animal Ecology*, **63**, 765–774.
- Wrona, F.J. & Dixon, R.W.J. (1991) Group size and predation risk: a field analysis of encounter and dilution effects. *The American Naturalist*, **137**, 186–201.
- Zuberbühler, K. (2009) Survivor signals: the biology and psychology of animal alarm calling. *Advances in the Study of Behavior*, **40**, 277–322.

Received 27 July 2014; accepted 11 February 2015

Handling Editor: David Reznick