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Convict cichlids benefit from close proximity to another species of cichlid fish

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The coexistence of species with overlapping resource use is often thought to involve only negative fitness effects as a consequence of interspecific competition. Furthermore, the scarce empirical research on positive species interactions has predominantly focused on sessile organisms. Here, I experimentally assessed the effect of close proximity of a potential brood predator and competitor on reproductive success of a neotropical cichlid fish. I demonstrate that convict cichlid (*Archocentrus nigrofasciatus*) broods have a higher survival rate near territories of the Nicaragua cichlid (*Hypsophrys nicaraguensis*), and that escape from predation and nest takeovers is the most likely explanation for the decreased offspring mortality.

Keywords: facilitation; offspring survival; positive interspecific interaction; predation avoidance; species coexistence

1. INTRODUCTION

For decades, ecological theory has been dominated by negative species interactions (Bertness & Callaway 1994; Bruno *et al.* 2003). Although interest in facilitative interactions between species has increased in recent years, most such studies have not been able to translate the perceived net benefits of interactions into fitness terms (Bruno *et al.* 2003). Furthermore, experimental research on positive interactions has mostly focused on plants and sessile animals and dealt with physical environment alteration and other by-product effects of actions of one species (Bertness & Callaway 1994; Stachowicz 2001). Nevertheless, behavioural interactions with members of another species may sometimes be beneficial, while costs of resource overlap and sexual competition are likely to be lower when interacting with heterospecifics. Behaviourally mediated benefits may come in the form of information use (reviewed in Seppänen *et al.* 2007), increased foraging efficiency (e.g. Bshary *et al.* 2006) or predator detection and avoidance (Dickman 1992). For example, mobbing behaviour of colonial birds may benefit neighbouring heterospecifics (Nguyen *et al.* 2006). Facilitative relationships can also have important community-level consequences, such as

changes in niche overlaps and species distributions (Bruno *et al.* 2003).

I tested the hypothesis, seeded by my own field observations, that close proximity to a breeding territory of the Nicaragua cichlid *Hypsophrys nicaraguensis* brings fitness benefits to breeding pairs of the convict cichlid *Archocentrus nigrofasciatus*. Such a positive relationship would be at odds with the predictions from classical ecological theory that focuses on the negative effects of competition and predation, especially since the two species commonly use the same breeding habitats where territory space is a limiting factor (McKaye 1977a), are likely to have overlapping diets especially at the juvenile stage and are potential predators of each other's juveniles (McKaye 1977a).

2. MATERIAL AND METHODS

The study was conducted in Lake Xiloá, Nicaragua, between December 2005 and January 2006 using SCUBA. The convict cichlid is dependent on pre-existing cavities for successful reproduction. Hence, I was able to manipulate the locations of their breeding sites by introducing artificial shelters, hereafter called nests, at the depths of 2–3 m. As nest sites, I used clay pots (roof diameter 5 cm, mouth diameter 9 cm) turned upside down with an entrance hole (5 × 2.5 cm). Breeding territories of Nicaragua cichlids were common at the chosen study site and were characterized by several deep pits excavated into the substratum, which consisted of soft silt and organic matter with patches of *Chara* green alga growing on it. Based on my preliminary observations, I considered the border of a territory to be drawn by the outer edges of the outermost pits. I placed each nest either within 1 m of, or farther than 2 m from, the border of the nearest occupied Nicaragua cichlid territory. Owing to the constant fluctuations in the number of Nicaragua cichlid territories at the study site, some nests were temporarily at a distance of more than 1 m but less than 2 m from the nearest territory. The way these nests are grouped does not qualitatively affect the results if not otherwise noted. For clarity, the results are given for the following two groups: nests that are close (within 1 m) and far (outside 1 m) from Nicaragua cichlid territories.

All nests were checked at least once a day for 5–7 days a week. A nest was considered to be colonized by a convict cichlid pair after eggs had been laid on its inner surface. I counted the number of eggs, caught the parents with a hand net to quickly measure them on the spot and then released them at the entrance of their nest. I followed the survival of the eggs and juveniles for the first 15 days after the eggs were laid (the fry start to swim after 6–7 days). This time period was chosen because thereafter the increased swimming capability of the juveniles entails a risk of misjudgement of their survival status. I used each nest location ($n=48$) only once in the experiment. For a subset of nests ($n_{\text{CLOSE}}=18$, $n_{\text{FAR}}=13$), I also measured the attack rate of the parents towards potential predators of the offspring (eleotriid *Gobiomorus dormitor* and all cichlid species in the lake) for 5 min after the pair had acclimatized to my presence for 3 min. In addition, I made similar observations for four Nicaragua cichlid pairs with convict cichlids nesting within 1 m from their territory. Most but not all of the broods were lost before 15 days had passed. Therefore, data on brood survival were analysed using log-rank survival analysis, which allows the inclusion of both kinds of replicates. Parametric statistical tests were applied only when their criteria were met. I used repeated-measures ANOVA to compare convict cichlids of the nests of the two treatments. The values of the two sexes of a pair comprised the 'repeated' dependent variable and the treatment (nest status) was used as a factor. Please note that it was possible for a nest to have a different status before and after it was colonized ($n=10$).

3. RESULTS

Nests within 1 m of Nicaragua cichlid territories received eggs in 4.0 ± 1.8 (mean \pm s.d., $n=23$) days, and nests further away in 4.4 ± 2.6 ($n=25$) days. This colonization pattern did not differ between the two nest categories (Mann–Whitney *U*-test: $U=291$, $p=0.94$). The standard length of convict cichlids

Table 1. Comparison of convict cichlids nesting within 1 m and further away from territories of Nicaragua cichlids using repeated-measures ANOVA. (Values of length and attack rate against predators are given as mean \pm s.d.)

variable	sex	nest status		effect						
		< 1 m	> 1 m	d.f.	sex		nest status		interaction	
					F	p	F	p	F	p
standard length (mm)	male	57 \pm 5.8	59 \pm 4.2	1,44	1476	0.000	1.39	0.24	1.10	0.30
	female	37 \pm 4.2	38 \pm 3.7							
attack rate (1 min ⁻¹)	male	1.7 \pm 0.92	1.7 \pm 1.3	1,29	11.7	0.002	0.101	0.75	0.131	0.72
	female	0.74 \pm 0.96	0.57 \pm 0.45							

colonizing nests within 1 m from occupied Nicaragua cichlid territories did not significantly differ from those colonizing nests further away (table 1; one female and one male were not caught), nor did the number of eggs laid in the nests differ (near: 125 ± 35 , $n=23$; further away: 131 ± 35 , $n=25$; two-sample t -test: $t_{46}=0.631$, $p=0.53$).

The survival rate of convict cichlid broods that were within 1 m from the nearest Nicaragua cichlid territory for more than half of the days before the whole brood was destroyed (or 15 days had passed) was higher than of the broods in nests that were further away for more than half of the days (log-rank test: Mantel-Haenszel, $\chi^2_1=7.03$, $p=0.008$; figure 1). Survival can also be measured on a day-to-day basis taking into account the daily status of each nest. Accordingly, the daily survival rate of broods within 1 m radius of an occupied Nicaragua cichlid territory was significantly higher than survival of those further away (96 versus 89%, G -test of independence: $G^2_1=5.47$, $p=0.019$). The effect was similar but not significant for a 2 m radius (94 versus 90%). Parents within and outside the 1 m radius did not significantly differ in their attack rate towards potential offspring predators (table 1). One of the four Nicaragua cichlid males was seen to direct aggressive behaviour twice towards a neighbouring convict cichlid pair swimming towards his territory (attack rate: 0.10 ± 0.20 min⁻¹, no attacks by females).

4. DISCUSSION

Close proximity to an occupied territory of Nicaragua cichlids resulted in fitness benefits for convict cichlids in terms of higher brood survival. To date, reports of such fitness benefits have been sparse (Bruno *et al.* 2003; but see, e.g. McKaye 1977b). I discuss three different, mutually non-exclusive explanations for the result. (i) Passive dilution of predation pressure equal to, or greater than that achieved in close proximity to conspecific breeding pairs. Any net benefit in the proximity of conspecifics seems very unlikely because reproductive success in the vicinity of other convict cichlid pairs has earlier been shown to be lower instead of higher (FitzGerald & Keenleyside 1978) and convict cichlids strongly avoid breeding in close proximity to each other (Lehtonen & Lindström 2008). A net benefit from passive dilution of predation in the proximity of Nicaragua cichlids cannot be ruled out, as the costs of breeding close to a heterospecific pair could be lower than in the proximity of other convict cichlids. However, if

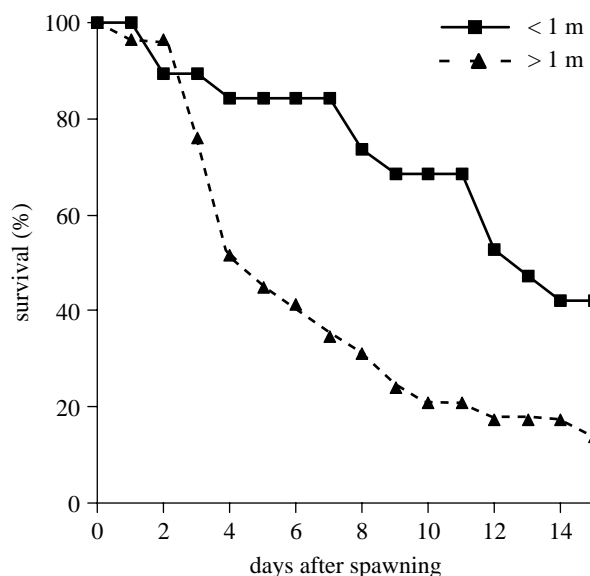


Figure 1. Survival of convict cichlid broods that were most of the time within the 1 m radius from the nearest occupied territory of Nicaragua cichlids ($n=19$, solid line) and outside of that radius ($n=29$, dashed line).

quantitative predation pressure was diluted, I would have expected to detect this as a lower encounter rate with predators, but this effect was not found. (ii) Shared optimal microhabitat: convict cichlids benefit when having their nest in the microhabitat chosen by Nicaragua cichlids. This explanation is unlikely because all nests were placed on an area known to be preferred by Nicaragua cichlids and the status of these territories was dynamic; breeding attempts of Nicaragua cichlids often failed in a few days and new territories were constantly being formed. Indeed, if all nests that had not been within a 1 m radius from a Nicaragua cichlid territory for a single day, either before or after the nest was colonized, are excluded, the difference between the two treatments remains statistically significant. (iii) Benefits mediated by behaviour of neighbouring Nicaragua cichlids, such as an increased effectiveness in avoidance of predation and nest takeovers. For example, Nicaragua cichlids seem to behave less aggressively towards their established neighbours than other convict cichlids (dear enemy phenomenon), which could result in reduced brood mortality due to nest takeovers for their neighbours. Given that the generally low nesting success of convict cichlid pairs is mostly due to high predation pressure and intense competition for

breeding shelters (McKaye 1977a), I consider the third explanation most important of the three. I did not find the *number* of aggressive encounters with predators to differ between the treatments. However, this does not mean that the *effectiveness* of predation repellence was necessarily the same. Indeed, qualitative rather than quantitative release from predation would point to benefits mediated by behaviour rather than dilution by numbers.

My observations point to interspecific specialization in predator repellence; convicts seemed to be more agile in chasing away small-sized offspring predators, while large Nicaragua cichlid males are able to attack any fish predator in the lake without being in the immediate risk of being consumed themselves (length distributions of the fish species in the lake in McKaye 1977a). The current evidence is uninformative about whether Nicaragua cichlid pairs also benefit from the convict cichlid pairs in the immediate vicinity of their territories. The low rate of aggressive behaviour of Nicaragua cichlid pairs towards their established neighbours suggests that at least there is no negative impact from their presence.

If it is beneficial to nest close to an occupied Nicaragua cichlid territory, why did convict cichlids not colonize these nests quicker than other ones? I offer three explanations that are not mutually exclusive. (i) Nicaragua cichlids initially behave aggressively towards convict cichlids that are not their established neighbours. This may slow down colonization of the nests near their territories. (ii) Breeding attempts of Nicaragua cichlids often fail (McKaye 1977a; T. K. Lehtonen 2005, personal observation), which means that the status of a given territory is dynamic. Hence, the probability of ending up as a neighbour of Nicaragua cichlids might be relatively constant across the spatial distances involved in this study, decreasing differences in popularity of the nests. (iii) Some pairs were seen in the vicinity of their chosen nest site before egg laying. To attain maximal objectivity, I did not consider a nest colonized before the eggs were laid. It is therefore possible that all nests were 'colonized' as quickly as females were able to produce eggs. In aquarium conditions, the mean time for newly paired convict cichlids to spawn was 8.24 days (Santangelo & Itzkowitz 2004).

Finally, I would like to note that the results of this study support the idea that conservation or management measures should be directed to whole habitats and communities living in them; positive species relationships may provide a crucial contribution to the functioning of the whole community (Cardinale *et al.* 2002; Seppänen *et al.* 2007). Moreover, the convict cichlid has been highly successful species invading numerous new communities where it has been introduced. One factor in the species' immense success may lie in the ability of breeding pairs to engage in commensal relationships with other fish species.

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