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Safety in numbers? Shoaling behaviour of the Amazonian red-bellied piranha

Helder Queiroz¹ and Anne E. Magurran^{2*}

¹Mamirauá Institute for Sustainable Development, Tefé, Amazonas CEP 69470-000, Brazil

²Gatty Marine Laboratory, University of St Andrews, St Andrews, Fife KY16 8LB, Scotland, UK

*Author for correspondence (aem1@st-andrews.ac.uk)

Red-bellied piranha (*Pygocentrus nattereri*) shoals have a fearsome reputation. However, the variety and abundance of piranha predators in the flooded forests of the Amazon in which they live indicate that an important reason for shoal formation may be predator defence. Experiments using wild-caught piranhas supported the hypothesis that individual perception of risk, as revealed by elevated ventilatory frequency (opercular rate), is greater in small shoals. Moreover, exposure to a simulated predator attack by a model cormorant demonstrated that resting opercular rates are regained more quickly by piranhas in shoals of eight than they are in shoals of two. Together, these results show that shoaling has a cover-seeking function in this species.

Keywords: selfish herd; cover seeking; schooling; risk-dilution; hyperventilation

1. INTRODUCTION

It is now well established that individual animals accrue significant anti-predator advantages by grouping with conspecifics; for example, in flocks of birds and schools of fishes (Elgar 1989; Magurran 1990; Pitcher & Parrish 1993; Cresswell 1994). However, although the protective properties of groups have been comprehensively investigated (Krause & Ruxton 2002), the individual decisions on which these advantages rest are much less well understood (Tien *et al.* 2004). Hamilton (1971) proposed that individuals take advantage of the cover provided by other group members to reduce their 'domain of danger'. The prerequisite for cover-seeking behaviour is a heightened perception of risk by singletons or members of small groups.

Few species have attracted greater notoriety than the red-bellied piranha, *Pygocentrus nattereri* (Schulte 1988). The species is popularly believed to be a dangerous pack-hunting fish. However, a recent investigation of the red-bellied piranha found no support for cooperative hunting and suggested that an important function of shoaling behaviour in the species is defence against predation (Magurran & Queiroz 2003). This assertion is supported by the observation that, in the flooded forests of the Brazilian Amazon in

which we work, piranhas are regularly preyed upon by river dolphins, caiman, aquatic birds and large piscivorous fishes (Bannerman 2001).

Here, we test the hypothesis that piranha shoaling is a form of cover seeking. We make two predictions: first, that fishes will feel safer in larger groups—as indicated by a reduction in their physiological stress response; second, that fishes in larger shoals will recover more quickly from a simulated predator attack. We use ventilatory frequency (opercular beat rate) as our measure of fearfulness. Previous work has demonstrated that opercular rate increases in fishes under predation risk; for example, in the presence of alarm substance (Pfeiffer 1962) or in response to a predator model (Metcalfe *et al.* 1987; Hawkins *et al.* 2004). Ventilatory frequency is thought to rise in anticipation of predator evasion (Barreto *et al.* 2003), even in the absence of prior locomotory activity.

2. METHODS

(a) Experiment 1: safety in numbers

We tested the prediction that piranhas perceive larger shoals as safer by measuring the opercular rate of fish as singletons and in shoals of two, four and eight individuals. The investigation took place at Flutuante Arapaima in the Mamirauá Reserve, Amazonas, Brazil. Piranhas are abundant in the flooded forest that comprises the reserve. Our study was conducted during the high-water season in July 2004.

Fish were collected between 12 and 24 h before testing and held in an underwater cage in their natural habitat so that stress levels were minimized. Trials were conducted in sets of four to ensure comparability of handling, time of day and so on. The order in which the four shoal sizes were tested within a set was varied across the 12 replicates in the experiment. Water was changed regularly. Oxygen levels, which were frequently monitored, did not fall below natural levels. At the beginning of a trial, a shoal of fish was gently placed in the test tank and allowed to settle for 10 min. A focal individual was then selected and its opercular rate measured for 5 successive minutes. Focal individuals, which could be identified by small variations in fin morphology, were chosen haphazardly. Using a single focal individual per group size ensured that the same number of observations was collected in each treatment. The tank was screened to avoid disturbance and all fish were observed from above. We selected the median of the five records of opercular rate per minute for our analysis. Afterwards, all fish were removed and measured, before being returned to the wild. With minor exceptions to make up shoal sizes (less than 2% of cases), fish were not reused. The mean (\pm s.d.) fork length of fish was 15.5 ± 2.09 cm.

(b) Experiment 2: response to predator 'attack'

We exposed piranhas in shoals of two and eight to a simulated attack from a realistic model cormorant, to test the prediction that larger groups regain their previous ventilatory rate faster than smaller groups. The oliveaceous cormorant, *Phalacrocorax olivaceus*, is an important predator of piranhas at Mamirauá (H. Queiroz and A. E. Magurran, personal observation). During each trial, the 75 cm-long model swooped from its perch and splashed into the water in the test tank ($60 \times 15 \times 60$ cm³ with water 20 cm deep). The model was then immediately removed. We recorded the opercular rate of a focal individual for five successive minutes after the attack. These values were contrasted with baseline opercular rate for the same focal individual, which had been measured for 1 min before the presentation of the model. There were 10 replicates per shoal size. No piranhas were tested more than once and different individuals were used in experiments 1 and 2.

3. RESULTS

(a) Experiment 1: safety in numbers

Our first experiment revealed a marked reduction in opercular rate with increasing group size (figure 1). A repeated-measures ANOVA on the untransformed data confirmed that the decline within sets was significant ($F_{3,33} = 12.67$, $p < 0.001$). *Post hoc* analysis

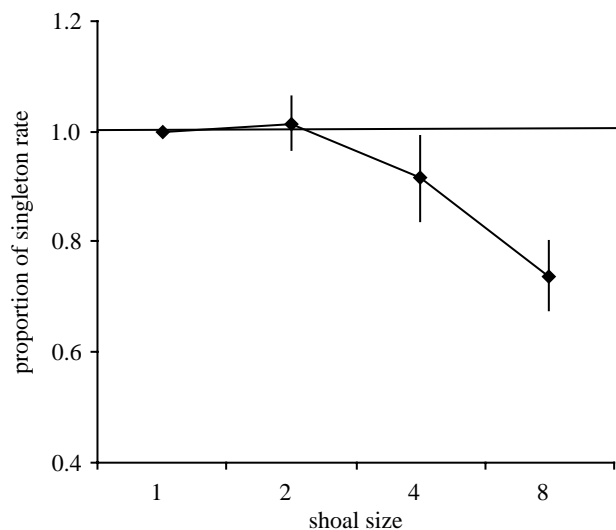


Figure 1. Opercular rate (per minute) of the focal individual as a proportion of the singleton's opercular rate (indicated by the line through unity) in a set of four tests. Mean value (\pm s.e.) is shown.

using the Bonferroni–Dunn test showed that there was no significant difference ($p > 0.05$) in opercular rate between singletons and groups of two, nor between groups of four and eight. The opercular rate in shoals of eight was 25% lower than for singletons. Overall, there was no relationship between the size of the focal individual and its opercular rate ($F_{1,46} = 0.005$, $p = 0.94$).

(b) *Experiment 2: response to predator 'attack'*

The second experiment took advantage of the observation that focal individuals in shoals of eight have a lower opercular rate than do individuals in shoals of two. Piranhas in both shoal sizes reacted vigorously to the predator model. Experiment 1 had shown that there was no trend in opercular rate over 5 min for groups of two and eight in the absence of direct threat: one sample t -test of slope coefficients of the relationship between opercular rate and time: shoal of two $t_{11} = 0.254$, $p = 0.80$; shoal of eight $t_{11} = 1.338$, $p = 0.21$. By contrast, opercular rates in was experiment, 2 increased dramatically following the presentation of the model (figure 2). We detected a significant difference between shoal sizes in response (repeated-measures ANOVA on proportion data: $F_{1,18} = 11.2$, $p = 0.004$) and a significant interaction between shoal size and time after presentation ($F_{4,72} = 4.77$, $p = 0.002$), indicating that the pattern of recovery also differed (figure 2). Opercular rates returned to the baseline levels more rapidly in the larger shoals.

4. DISCUSSION

The popular image of red-bellied piranhas portrays them as more feared than fearful. However, the results of our investigation are consistent with an anti-predator function for shoaling in the species. We found that opercular rate, which typically increases under risk (Metcalf *et al.* 1987; Barreto *et al.* 2003), and may be indicative of a fish's preparedness to flee (Hawkins *et al.* 2004), was lower in larger groups,

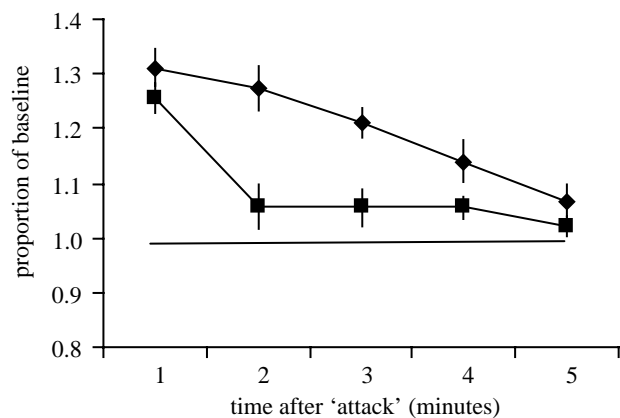


Figure 2. Mean opercular rate (\pm s.e.) of the focal individual in shoals of two and eight, in the 5 min period following predator attack, as a proportion of its baseline value (indicated by the line through unity). Diamond symbols represent shoals of two, and square symbols represent shoals of eight.

even in the absence of an overt predation threat. Furthermore, after a simulated attack, opercular rate remained elevated for longer in the smaller shoals. Because the size of red-bellied piranha shoals at Mamirauá ranges from fewer than 10 to about 100 (H. Queiroz and A. E. Magurran, personal observation), the grouping advantages detected in this experiment are applicable to fishes in the wild. Our study not only casts new light on the behaviour of a charismatic, though poorly researched species, but also reveals how a fish's perception of risk is affected by shoal size.

In the flooded forest at Mamirauá, shoals of fishes (including piranhas) are constantly under risk of attack. A large body of literature attests to the many anti-predator advantages enjoyed by larger groups (Krause & Ruxton 2002). In addition to increased vigilance, there are benefits related to dilution and predator confusion. The probability that a predator will successfully capture a fish declines with shoal size (Neill & Cullen 1974). For these reasons fishes seek cover by placing themselves next to other individuals (Williams 1964; Hamilton 1971; Williams 1992). Previously, we showed that large, reproductively mature piranhas position themselves in the centre of a shoal, and take fewer risks than smaller, immature individuals during foraging (Magurran & Queiroz 2003). The present study strengthens the conclusion that individual piranhas join shoals to reduce their risk of capture. In our study, we examined fish that had no cover from the simulated predation attack. However, piranha shoals may occur in the flooded forest itself as well as in open water in Mamirauá lake, and it is probable that they use the cover provided by submerged branches to evade predators. It would be interesting to determine whether the benefits of shoaling as a cover-seeking device reduce in the presence of physical cover to shelter in.

Time devoted to predator avoidance is time lost from other activities such as foraging. This trade-off can be optimized by resuming previous behaviour as soon as possible after the threat has abated (Krause & Ruxton 2002). For this reason, membership of

a larger shoal provides advantages over and above the differences in baseline ventilation frequency. Because higher opercular rate is associated with higher metabolic rate (Shelton 1970; Olson 1998), piranhas in smaller shoals probably also experience greater oxygen requirements. Physiological costs could be particularly significant in this habitat as the flooded forest is seasonally affected by low levels of dissolved oxygen, a result of high rates of decomposition (Henderson *et al.* 1998). Periodic mass fish kills are a natural phenomenon here (Henderson *et al.* 1998). Individual mysids (*Euphasia superba*) consume less oxygen in larger swarms than in small groups (Ritz 2000), even when performing escape responses (Ritz *et al.* 2001). Our results point towards a similar benefit in piranhas.

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