

CAN AGGREGATION BEHAVIOUR OF *PHRYNOMANTIS MICROPS* TADPOLES REDUCE PREDATION RISK?

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In the Comoé National Park in Ivory Coast, West Africa, tadpoles of the microhylid frog *Phrynomantis microps* often stay in large and densely packed aggregations near the water surface of savanna ponds. Previous studies have shown that aggregation behaviour was initiated by the presence of visually guided aquatic predators. In the present study, I investigated how efficiently aggregation of *P. microps* tadpoles reduces the risk of predation. I used an experimental design to count the number of attacks by predators on *P. microps* tadpole at different densities and distributions. The total strike rate of predators was significantly lower when *P. microps* tadpoles were aggregated than when they were randomly distributed. However, per capita strikes rate did not differ between treatments. Further replicate trials might have detected benefits to the individual tadpole from aggregating.

Keywords: anti-predation behaviour, anurans, dilution effect, social behaviour

INTRODUCTION

Animals of many species live together in groups for the whole life span or, more often, for a particular period. Group members may experience increased foraging efficiency (Beiswenger, 1975), prevention of desiccation (Heinen, 1993), increased reproduction possibilities (Ryan *et al.*, 1981) or reduced risk of predation (Hamilton, 1971; Bertram, 1978; Pulliam and Caraco, 1984). There are three different ways in which grouping may help to reduce rates of successful attack by predators. The dilution effect is a numerical phenomenon with the result that in a larger group an individual has a lower risk of being taken (Foster & Treherne, 1981; Turner & Pitcher, 1986; Coster-Longman *et al.* 2002). The confusion effect provides safety by increasing the number of capture mistakes by predators against a larger group size of the prey (Milinski, 1979; Landeau & Terborgh, 1986; Krakauer, 1995). The Trafalgar effect reduces risk of predation in groups by cooperative behaviours of the prey such as abrupt changes in speed of movement or rapid disappearance of the aggregation after only a few members of the group detect a predator (Treherne & Foster, 1981).

Numerous studies have shown that one or more of these three effects are responsible for the aggregation behaviour in any particular species, but only a few experimental studies have quantified the individual survival rate of prey corresponding to their distribution pattern (e.g. Watt *et al.*, 1997).

In the Comoé National Park, West Africa, *Phrynomantis microps* tadpoles form aggregations near the surface of ephemeral savanna ponds (Rödel & Linsenmair, 1997; Spieler, 2003). Previous experiments in containers with clear water demonstrated that the aggregation behaviour of *P. microps* tadpoles was only shown while predators were present and was induced by

visual detection of the predator or by chemical cues (Rödel & Linsenmair, 1997). Each tadpole in such an aggregation floated nearly motionless until disturbed by a predator attack. Then, all tadpoles quickly dispersed, triggered by initial swimming activity from a few tadpoles close to the centre of the disturbance.

In this study, I used an experimental design to investigate how efficiently the aggregation of *P. microps* tadpoles reduces the risk of being preyed upon. The design was chosen to test only the dilution hypothesis.

METHODS

STUDY AREA

The study area is situated in the Guinean savanna of Comoé National Park (8°5'-9°6' N, 3°1'-4°4' W) in the north-eastern part of the Ivory Coast (West Africa). This region is characterized by distinct wet and dry seasons, with a mean annual precipitation between 750 and 1100 mm during 1994 and 2001 (measurements of the research camp in Comoé National Park). The core dry period, lasting from December to February, usually lacks precipitation. Most bodies of water in the study area are ephemeral ponds that always dry up in the dry season. *Phrynomantis microps* breeding ponds do not usually fill before April or May.

STUDY ANIMAL

Phrynomantis microps Peters, 1875 is a medium-sized microhylid frog of the West African savanna. Breeding occurs throughout the rainy season in ephemeral savanna ponds (Rödel, 2000). The tadpoles are barely pigmented and thus very translucent (Rödel & Spieler, 2000). They are suspension feeders with a specialized filter apparatus.

GENERAL METHODS

I conducted the experiments in the research camp in Comoé National Park between 1-15 August 1999. I used a transparent plexiglass floating arena (35 × 20 × 4

cm) with 40 compartments to quantify the strike rate of predators presented with different tadpole densities and distributions. Each compartment ($4.9 \times 3.3 \times 4.0$ cm) was large enough to allow 10 medium sized *P. microps* tadpoles to maintain tadpole-tadpole distances similar to that measured in large aggregations of more than 100 individuals from natural ponds. Standard capped plastic vials used for 35 mm film were attached to two sides for buoyancy. This arrangement was similar to that used by Watt *et al.* (1997). The arena was floated in green plastic containers (45 x 35 x 25 cm) that were filled to a depth of 8 cm with clear water from rock pools and savanna ponds.

I used carnivorous tadpoles of *Hoplobatrachus occipitalis* and killifish *Nothobranchius kiyawensis* of similar size as predators. Both predator species are natural predators of *P. microps* tadpoles and show a similar hunting strategy. This made it possible to use both predators together in the experiments in view of the very low abundance of both predator species during the study period. The predators were kept in a large aquarium 24 hr before the experiment started and were fed with mosquito larvae. The feeding did not occur *ad lib* so that the predators reacted with the same intensity to the addition of new mosquito larvae. One carnivorous tadpole and one killifish were chosen randomly and transferred to each of six containers 10 hr before I presented the arena to the predators. I never saw any kind of interaction between the predatory tadpole and fish.

The experimental herbivorous *P. microps* tadpoles I used had a snout-vent length of 6.0-9.4 mm and were at developmental stages 25-36 (Gosner, 1960). These tadpoles were netted in one savanna pond and kept together in one aquarium 24 hr before the experiment started. They were fed with a suspension of algae.

Each of the 13 experiments involved testing six trials in succession during a single day. The floating arena was placed into one of the six containers and the *P. microps* tadpoles were pipetted into the arena according to one of the following treatments: (1) one tadpole, randomly placed in the arena; (2) five tadpoles, each in one compartment; (3) five tadpoles, together in one compartment; (4) 10 tadpoles, each in one compartment; (5) 10 tadpoles, together in one compartment; (6) no tadpoles. The compartments used in each arrangement were chosen randomly. Transferring 10 tadpoles took 2-3 min. After recording, the arena was cleaned, placed into the next container and another set of tadpoles were transferred using the arrangement described above. The sequence of allocation was assigned randomly.

After an acclimation period of 10 min with the predators, I recorded in each trial the number of strikes the predators made against the experimental tadpoles, making observations from a 45° angle above the arena over a 10 min period. This observer position allowed me to see through the arena with the experimental tadpoles to the base of the container where the predators were contained. Without the presence of prey, both predator

species stayed motionless on the bottom of the container most of the time, sometimes for over one hour.

I counted an attack of a predator against the experimental tadpoles as one strike if it touched the bottom of the floating arena. To discriminate an attack from other rare behaviours in which predators touched the bottom of the arena (e.g. swimming to the water surface to swallow air), I defined the following behavioural sequences as an attack: (1) if a *Hoplobatrachus occipitalis* larvae swam from the ground of the container directly to a *P. microps* tadpole, turned on its back and touched with an open mouth the transparent base of the floating arena that physically separated the predator from the experimental tadpole. After the unsuccessful attack the predatory tadpole sank back to the bottom, (2) if a *P. microps* tadpole was detected, the killifish straightened up in a sloping position and swam very slowly towards the prey. Thereby, the predator compensated all movements of the tadpole by concomitant changes of direction during its approach until it touched the base of the arena below the tadpole.

At the end of each trial I obtained the number of strikes of the two predators against the 1 to 10 prey-tadpoles in different distribution patterns. The mean per capita strike rate was calculated by dividing this number by the number of tadpoles that were present in that trial. To test for statistical differences between numbers of strikes depending on different densities and distributions of tadpoles, data from treatments 1 to 5 were compacted and calculated by a one way repeated measure ANOVA (StatView 5.0 for Macintosh).

The *P. microps* tadpoles did not react to the predators' attacks. They were never injured and showed no signs of distress. In correspondence with the behaviour of this tadpole species in natural ponds, experimental tadpoles stayed motionless most of the time floating on the water surface of their compartment. From this position there was a distance of about 3 cm to the bottom of the container and therefore from the predator if it touched the base of the arena. Obviously, the visual recognition of a predator's attack alone seems insufficient to initiate a flight reaction in *P. microps* tadpoles.

At the end of the experiments all tadpoles and fishes were returned to their natural pools.

RESULTS

In control trials (treatment 6) where no tadpoles were placed in the arena, no predator attacks were recorded. These trials, which were meant to serve as a baseline, were thus omitted from the analysis.

The total number of strikes towards the arena differed between experimental treatments (ANOVA: $F_{4,48} = 10.4$, $P < 0.001$). Fischer's PLSD posthoc tests show that the total strike rate of predators towards tadpoles that were isolated in separate compartments increased with the total number of tadpoles in the arena (Fig. 1, Table 1). For aggregated tadpoles, however, no significant density effect was seen between the two treatments (Fig. 1, Table

TABLE 1. Results of the posthoc test for differences between numbers of strikes towards the arena in dependence on the different densities and distributions of tadpoles.

Fisher's PLSD: total strike rate	Mean. diff.	<i>P</i>
1 vs. 5 aggregated	-1.15	0.45
1 vs. 5 random	-2.85	0.06
1 vs. 10 aggregated	-2.15	0.16
1 vs. 10 random	-6.08	0.0002
5 random vs. 5 aggregated	1.69	0.27
5 random vs. 10 random	-3.23	0.04
5 aggregated vs. 10 aggregated	-1.00	0.51
10 random vs. 10 aggregated	3.92	0.01

1). Most notably, the posthoc test revealed that fewer attacks were directed towards the arena when ten tadpoles were clumped in one compartment than when ten tadpoles were randomly distributed in different compartments.

Analyzing the per capita strike rates (Fig. 2) by ANOVA, there was no statistical difference between the five treatments ($F_{4,48}=0.95$, $P=0.44$).

DISCUSSION

The present study demonstrates that larger groups are more frequently attacked by predators than smaller ones. This is consistent with the encounter effect where

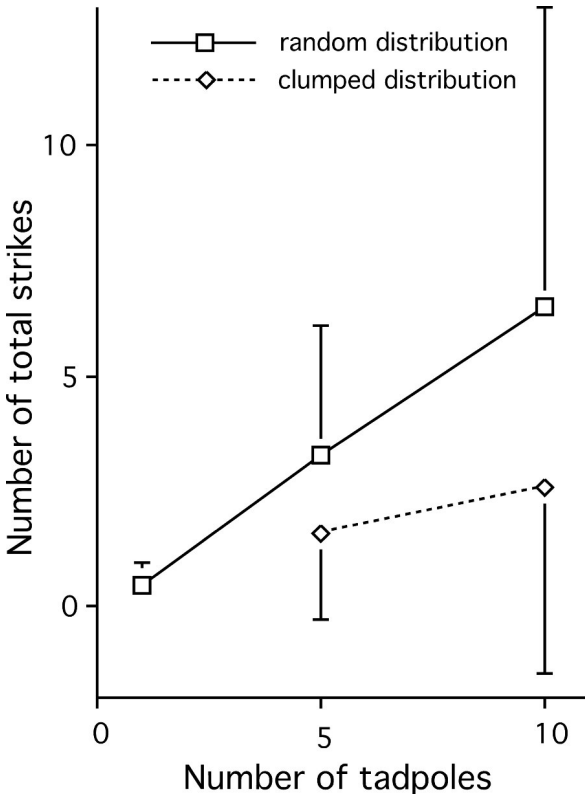


FIG. 1. Relationship between the mean number of total strikes of the predators towards the arena and the number of tadpoles present (either aggregated in one compartment or randomly distributed across the 40 compartments). Standard deviations are given as either positive or negative error bars. Each point represents the mean of 13 observations.

larger groups are more likely to be detected by a predator and are more attractive than smaller ones (Siegfried & Underhill, 1975; Watt & Chapman, 1998). The key factor seems not to be aggregation size *per se*, but the stronger movements in larger groups (Krause & Godin, 1995). Models that combine the encounter effect with the counteracting dilution effect indicate that protection against predators or parasites is provided when the probability of detection of a group does not increase in proportion to the increase in group size (Turner & Pitcher, 1986; Wrona & Dixon, 1991; Mooring & Hart, 1992). Evidence of such antagonistic relations between encounter and dilution effects is given for some species (Duncan & Vigne, 1979; Foster & Treherne, 1981; Cresswell, 1994).

In correspondence with the combined models, I found increasing total strike rates of predators with increasing density of prey tadpoles, but also a significant difference in total strike rate of predators between clumped and randomly distributed tadpoles at high equivalent densities (Fig. 1). Thus, highly aggregated tadpoles were less often attacked than the same number of randomly distributed tadpoles.

The risk of being preyed upon for an individual tadpole did not differ significantly between clumped and random distributions. However, the low statistical power warrants caution for this conclusion, and the ac-

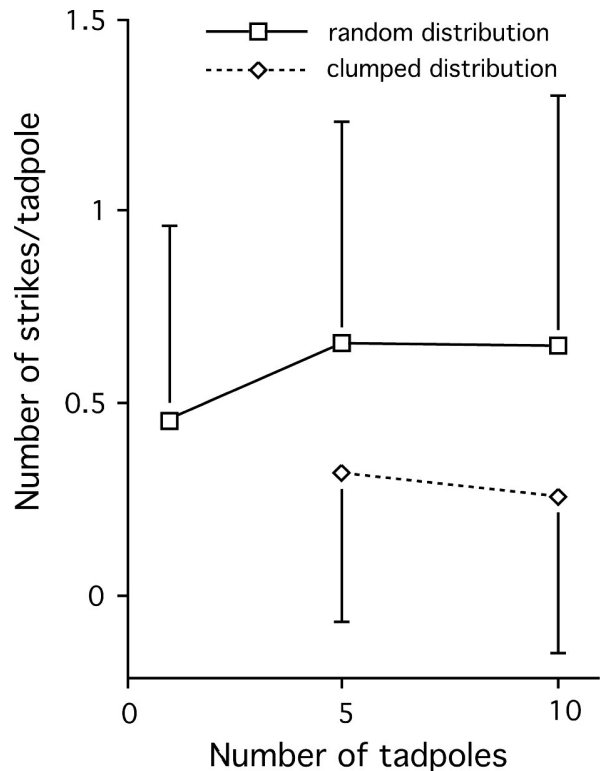


FIG. 2. Relationship between the mean number of per capita strikes of the predators towards the arena and the number of tadpoles present (either aggregated in one compartment or randomly distributed across the 40 compartments). Standard deviations are given as either positive or negative error bars. Each point represents the mean of 13 observations.

tual data (Fig. 2) suggest that more replicate trials might have detected benefits to the individual tadpole from aggregating.

The advantage for aggregated *P. microps* tadpoles is probably not simply a result of the dilution effect but, additionally, might be caused by the particular foraging behaviour of the predators. The hunting strategy of both the predators used can be classified as a sit-and-wait strategy. These predators mostly lay motionless on the base of the container and moved only occasionally and slowly through the water. The translucent tadpoles swimming on the water surface can only be detected by predators at a short distance. The probability of reaching such a distinct area in which a predator can detect one single tadpole or one dense aggregation depends on the intensity of the predator movements. For example, the chance for a sit-and-wait predator staying in a pond with two prey tadpoles to detect one of these tadpoles when they were randomly distributed is much higher than to detect these two tadpoles when they are in a group. By contrast, the chance for highly mobile predators to detect one of two randomly distributed tadpoles or these two tadpoles when they are in a group seems to be nearly the same. This applied especially if tadpole species are less conspicuous and if the attractiveness of an aggregation increased to a lesser extent than the increase in group size.

As most potential tadpole predators in the savanna ponds of the study area are sit-and-wait predators (Rödel, 1998), this hunting strategy provides an additional incentive for *P. microps* tadpoles to form large aggregations under high predation pressure. The importance of the hunting strategy of predator species on the survival rate of aggregated prey and thus on the constraints for prey to aggregate in the presence of predators with a defined foraging strategy has been pointed out in different studies (Parrish, 1993; Cresswell *et al.* 2003).

Furthermore, as the investigated predators of *P. microps* tadpoles visually orient towards – and attack – individual prey items, they may be subject to the confusion effect (Neill & Cullen, 1974). This probably leads to a further advantage of being aggregated in this species but was not quantified in this study. Likewise, it is to be expected that the Trafalgar effect plays an important role as an anti-predator strategy. This was indicated by the observed rapid synchronous flight reactions of *P. microps* tadpoles to dissolve aggregations once attacked by the predator *H. occipitalis* and by the ascertained sensitivity towards conspecific alarm substances (Rödel & Linsenmair, 1997).

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