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Is there always an influence of shoal size on predator hunting success?

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Theoretical and empirical studies predict that there should be a decrease in hunting success of predators with increasing prey group size. Most of these studies investigated situations in which predator and prey were in full view of each other before, during and after an attack. In this study, single rock bass *Ambloplites rupestris* were given an opportunity to launch surprise attacks at shoals of creek chub *Semotilus atromaculatus* that ranged in size from two to 13 fish. There was no significant influence of either shoal size or attack distance on predator success rate and no significant relationship between attack distance and shoal size. Furthermore, it was found that the leading fish of a shoal was attacked significantly more often than fish in other shoal positions, indicating that predation risk was not shared equally among shoal members. Also, leading fish in larger shoals (eight to 13 fish) were not more likely to survive a predator attack than ones in small shoals (two to seven fish). The consequences of these results are discussed in the general context of antipredator benefits of grouping.

Key words: shoaling behaviour; predation risk; attack distance; *Ambloplites rupestris*; *Semotilus atromaculatus*.

INTRODUCTION

Many experimental and theoretical studies have provided evidence for antipredator effects of group-living in animals (Neill & Cullen, 1974; Pulliam & Caraco, 1984; Godin, 1986; Turner & Pitcher, 1986; Pitcher & Parrish, 1993; Godin, 1997). The predator confusion effect (Milinski, 1977), the encounter-dilution effect (Turner & Pitcher, 1986) and early predator warning (Magurran *et al.*, 1985) are just a few of those factors believed to give protection to prey groups from predators (Pitcher & Parrish, 1993; Godin, 1997). The predator confusion effect is based on the idea that it becomes increasingly difficult for predators to pick out individual prey from prey groups because the choice between many moving targets creates sensory overload of the visual channel (Broadbent, 1965; Krakauer, 1995). Groups often detect predators earlier than solitary individuals, thus increasing the likelihood of successful escape (Magurran *et al.*, 1985). The encounter-dilution effect is based on a combination of detection and attack probabilities. It is advantageous for an individual to be in the larger of two groups if the probability of detection and subsequent attack by the predator does not increase over-proportionately with increasing group size (Turner & Pitcher, 1986).

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Most of the studies that have investigated how predator success decreases with increasing group size have focused on situations in which predator and prey were in clear and continuous view of one another before, during and (in the case of repeated attacks even) after the attack (Neill & Cullen, 1974; Major, 1978; Landeau & Terborgh, 1986; Krause & Godin, 1995). Potentially, this visual contact gives prey groups an opportunity to prepare themselves for an attack by aggregating more closely and to predict the timing of an attack (Godin, 1997). In this paper, a scenario was investigated in which the prey group could not see the predator before the attack but the predator could watch the prey. The question was whether hunting success of predators still decreased with increasing prey group size when a predator could launch a surprise attack. Additionally, which shoal positions were most often attacked and therefore incurred the highest predation risk was also examined. If, as assumed in Hamilton's (1971) selfish herd model, a predator strikes at the closest prey then this should put the leading fish at the highest risk for mobile groups because usually it will be the first one to come within the predator's attack range (Bumann & Krause, 1993; see Bumann *et al.*, 1997 for a simulation model of this scenario).

MATERIALS AND METHODS

Several hundred creek chub *Semotilus atromaculatus* (Mitchill) (mean ± S.D. standard length 4·0 ± 0·1 cm) were taken with a beach seine from shallow pools and 10 rock bass *Ambloplites rupestris* (Rafinesque) (13·2 ± 0·9 cm) were caught with hook and line from Stony Brook (Princeton, New Jersey, U.S.A.). Rock bass were fed on freeze-dried euphausiid shrimps and creek chub, but were deprived of food 24 h prior to being used in the experiments. Creek chub were kept in holding tanks at 15° C and fed *ad libitum* on Tetramins™ flakes twice daily for several months before being used in the experiments. Previous studies using creek chub from the same location indicated that shoaling plays an important role as an antipredator behaviour in this species (Krause *et al.*, 1997, 1998). Creek chub were observed to form shoals in the wild which range from just a few individuals to several hundred fish and juveniles usually occur in the littoral zone under conditions which can be approximated relatively easily in the laboratory (Krause, unpublished data). Stony Brook is rich in predatory fish species including pike *Esox* sp., largemouth bass *Micropterus salmoides* (Lacépède), crappie *Pomoxis* sp., rock bass, bluegill *Lepomis macrochirus* (Rafinesque), pumpkinseed, *L. gibbosus* (L.), and green sunfish *L. cyanellus* (Rafinesque). Several species of piscivorous birds such as kingfishers and herons were observed also.

The test pool was 120 cm in diameter (15 cm water depth) and the water temperature was maintained at 15° C. The light : dark regime (12 : 12 h) was determined by artificial lights (neon tubes) suspended *c.* 2·5 m above the test tank. In each trial, 13 chub were chosen randomly from the holding tank and introduced to the test pool using a transparent plastic cylinder (15 cm in diameter). The chub were able to view their surroundings from inside the cylinder for about 3 min and then released by lifting the cylinder with a remote pulley mechanism. On the side opposite to where the chub were introduced, a rock bass was positioned in a hide (see Bumann *et al.*, 1997 for further details of the experimental set-up). The hide consisted of a black floating rectangular plastic sheet that was folded several times giving it a surface area of 15 × 20 cm. The bass was introduced to the pool 24 h prior to the introduction of the prey fish, positioned itself inside the hide within a few seconds of introduction, and always stayed there throughout a trial except when making its brief attack on the chub. Due to an inverted opaque bowl ($L \times W \times H$: 50 × 25 × 20 cm) in the middle of the pool, the chub were not able to view the hide while they were inside the plastic cylinder. To see the hide, the chub had to swim around the bowl to the other side of the pool. The rock bass was always well hidden inside the black plastic folds and the chub did not avoid the hide or hesitate to approach. Thus there was no indication that they detected the bass before they were attacked by it. However, the possibility cannot be excluded that chub detected the presence of the bass in the tank through olfactory cues. This might alert the fish to the presence of a predator but would be unlikely to give information about its precise location (Smith, 1997).

The chub's approach to the hide was recorded using a video camera 1·5 m above the pool. Shoal size, attack distance (distance between the bass and the individual prey fish that was attacked), outcome of the attack (successful or unsuccessful capture of a fish) and shoal position of the fish that was attacked were all recorded in each trial. In over 70% of trials, shoals split into subshoals before approaching the hide which is why shoal sizes (under attack by the bass) varied from two to 13 fish (mean nine fish). The variability in shoal size was beyond experimental control because the 13 fish could split up into a number of subshoals after release from the cylinder. Whenever this happened, the predator attacked the first shoal that came within reach (maximum attack distance was 6 cm). The predator never left its hide to approach a shoal before launching an actual attack. Similarly, it never passed up an opportunity to attack a shoal that came within 6 cm. Therefore there was no element of shoal choice by the predator.

The bass attacked the shoal by launching out of its hide for a brief moment and then returning immediately, irrespective of whether the attack was successful or not. The bass did not pursue the shoals through the pool and the shoal was removed immediately after the first attack by the bass to minimize the stress for the prey fish. The bass never captured more than one single fish in a given attack and the shoal usually left the area quickly after the attack. Attack distance was estimated to the nearest cm from a grid on the bottom of the pool. Three trials with each of 10 bass made a total of 30 trials. The same bass was used not more than once in a 7-day period. Individual chub were used not more than once.

The lead position in a shoal of chub was defined as the position in which a fish was at least half a body length in front of any other fish in the direction of the general swimming direction of the shoal. If the distance was smaller than half a body length, the lead position was defined as being shared by two (or more) fish (only two such instances occurred in our data set).

To investigate the relationship between predator success and prey shoal size, a logistic regression analysis was used of the form: $\log(P(P-1)^{-1})=a+bS+cD$, where P is the probability of being eaten, S is shoal size and D is attack distance. Best fits for parameters b and c were then calculated.

RESULTS

Overall, rock bass attacked chub shoals successfully in 56% of the trials. No evidence was found that either size of the prey group or the distance from the predator to prey when the attack was initiated affected the success of an attack (logistic regression, both coefficients not significantly different from zero: $b=-0{\cdot}07$, S.E.$=0{\cdot}11$, approximate 95% confidence interval for $b=-0{\cdot}29$ to $0{\cdot}15$, $P=0{\cdot}63$; $c=0{\cdot}36$, S.E.$=0{\cdot}39$, approximate 95% confidence interval for $c=1{\cdot}14$ to $-0{\cdot}42$, $P=0{\cdot}23$). Furthermore there was no significant correlation between shoal size and attack distance (Fig. 1).

The lead fish was singled out for attack much more than would be predicted by the null hypothesis that the predator selected its target randomly from the group (Table I). In the 22 trials with shoal sizes <12, the lead fish was the one attacked in every case. For shoal size 12, only three trials were available. The null hypothesis of random selection suggested that the probabilities of observing the lead individual being attacked in zero, one, two or three of these trials were 78, 20, 2 and <0·1% respectively. The leader was attacked in only one trial which is

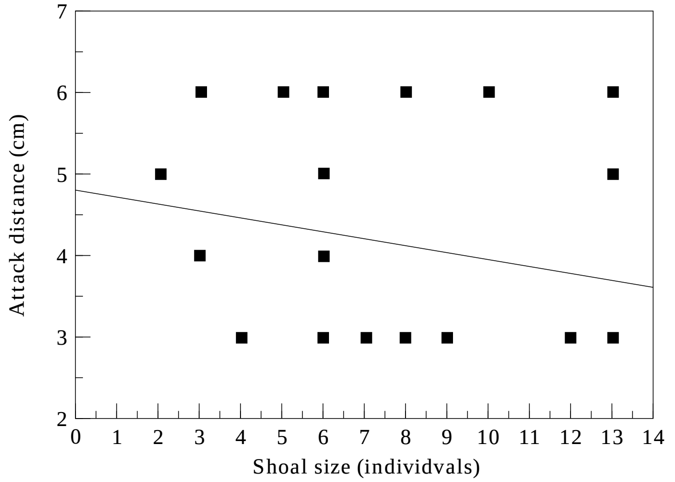

FIG. 1. Attack distance in relation to shoal size for all 30 cases in which rock bass attacked shoals of chub. Linear regression: $y=4{\cdot}794-0{\cdot}083x$; $r^2=0{\cdot}049$, $P=0{\cdot}24$.

TABLE I. Predation risk and group size

Group size	Total trials	Trials when leader was attacked	Trials when leader was eaten
2	1	1	1
3	2	2	1
4	1	1	1
5	1	1	1
6	4	4	4
7	2	2	0
8	6	6	2
9	1	1	0
10	1	1	1
12	3	1	1
13	8	7	4
Total	30	27	16

suggestive that the null hypothesis might be invalid, but not significantly so. However, the eight trials with shoals of 13 fish in which all but one of the trials saw the front fish targeted are conclusive. The binomial probability of this occurring based on the null hypothesis is <0·0001%. Hence, all the data suggest clearly that the fish in the lead position was considerably more at risk than individuals in any other shoal position.

It cannot be demonstrated that the probability of the lead fish being targeted is related to shoal size, since non-leading fish were selected in only three cases out of thirty. It might be important that these three occasions occurred at larger group sizes (12, 12 and 13). However, this should be set against the observation that in seven of the eight trials with the biggest shoal size, the lead fish was targeted.

Again, because of the small number of occasions when non-leading fish were targeted, it cannot be explored whether leading fish are more or less likely to survive an attack than other shoal members. However, it can be tested whether leading fish in larger groups are more or less likely to escape attack than those in smaller groups. Shoals of two to seven individuals were defined as small shoals, and those of eight to 13 individuals as large ones. In small shoals, the leading fish got eaten in eight cases and survived in three and in large shoals it got eaten in eight cases and survived in eight which indicates that there is no significant relationship between shoal size and the leading fish's likelihood of surviving an attack (Fisher's exact test, $P=0{\cdot}21$). Thus leading fish in large shoals had a slightly lower predation risk than ones in small shoals (difference between proportions of fish getting eaten in large and small shoals $= -0{\cdot}23$, S.E. $=0{\cdot}19$, approximate 95% confidence interval $-0{\cdot}61$ to $0{\cdot}15$). However, the large S.E. indicates that the power of the Fisher's exact test is not very strong given the relatively small sample size.

On two occasions, two fish were so close together at the front of the shoal that both had to be classed as leading fish. This occurred once in a shoal of five and once in a shoal of six fish, on both occasions one of these fish was attacked successfully. The above analysis classifies these two fish as front fish, although none of our conclusions would be changed if these fish were reclassified as non-leading.

DISCUSSION

The results of this study do not show a significant relationship between shoal size and predator hunting success, in contrast to numerous other studies which reported that predator success declined with increasing shoal size (Neill & Cullen, 1974; Major, 1978; Landeau & Terborgh, 1986; Krause & Godin, 1995). The absence of such a relationship in our study could be due to the absence of visual contact between predator and prey; i.e. given a surprise attack, shoaling may not be as effective as an antipredator strategy. For this idea to be investigated further one would need a control in which rock bass and chub shoals are in clear view of each other before and during an attack. If predator success declines significantly with increasing shoal size in this situation, this would give strong support for the idea that antipredator benefits of grouping depend crucially on prey having visual contact with its predator. One of the reasons why visual contact might be so important is that fish shoals aggregate more strongly and stop searching for food once they have detected a predator. Furthermore, they can monitor the predator's behaviour and predict the timing of an attack thus increasing their chances of successful escape (Pitcher & Parrish, 1993; Godin, 1997). Alternatively it is possible that rock bass are generally very highly successful predators irrespective of whether they have been detected by prey. A success rate of 56% as reported in this study is close to that of black skipjack *Euthynnus lineatus* Kishninouye (70–75%), which is among the most successful piscine predators that attack fish shoals (Parrish, 1993). High success rates by predators are known to be achieved in a number of different ways. Species such as jacks often hunt in groups and split up prey groups by bursting into them at high speeds. They then pursue individual prey which are easier to catch (Major, 1978). Other predators such as sawfish (genus *Pristis*) stun their shoaling prey with quick strikes of their saws (Breder, 1967). Here, surprise attacks could be another effective strategy employed by predators to catch grouping prey. This is a strategy not available to the same extent to the aforementioned species (jacks and sawfish) because as predators of pelagic prey they hunt in the open water where surprise attacks from cover are not possible.

The shoal sizes used in this paper correspond to those investigated in other studies (Landeau & Terborgh, 1986; Krause & Godin, 1995) in which a strong decrease in predator hunting success with shoal size was observed. Landeau & Terborgh (1986) found that fish in shoals of two or four were significantly more vulnerable to predation than individuals in shoals of eight fish. Krause & Godin (1995) reported that the probability of successful capture of a prey fish decreased significantly with increasing shoal size investigating shoal sizes ranging from one to eight fish. Thus, a similar trend could be expected in our data.

As mentioned earlier, the possibility that chub had information about the presence of a predator in these experiments cannot be fully disregarded. Recent experiments have shown that prey fish can detect the presence of predators based on olfactory cues (Smith, 1997). However, it seems likely that the chub's response to olfactory cues alone, if they were present, should be less strong than that to olfactory plus visual cues. Irving & Magurran's (1997) work indicates that olfactory cues are not always sufficient to elicit antipredator behaviour in fish shoals and suggests that additional visual cues are important (Magurran *et al.*, 1996). Furthermore, olfactory cues do not provide information about the exact timing of a predator's attack, as do visual cues (Godin & Morgan, 1985). In any case, whether or not fish had detected the presence of a predator based on olfactory cues still does not change the fact that there was no relationship between shoal size and predator hunting success. Therefore, even if chub had detected the predator's presence this information obviously did not bring about a significant decrease in the predator's hunting success with increasing shoal size.

Interestingly, even if shoaling does not reduce the predator's success rate it could still be advantageous for fish to be in groups for reasons outlined by Hamilton (1971). According to Hamilton, singletons would have a much larger domain of danger (probability of being the closest prey to a predator) than shoaling individuals, and thus there would still be selection for shoaling. Hamilton's model also implied that individuals at the periphery of a group incur higher risks of being attacked and eaten than do central individuals. This idea was further developed by Bumann *et al.* (1997), who quantified the predation risk for individual group members in moving groups, as opposed to stationary groups in Hamilton's original model. The simulation of Bumann *et al.* (1997) predicted a strong positive risk gradient from the back to front of a moving group. The data presented in this study are consistent with this prediction in that the leading fish of a shoal was at a significantly higher risk than individuals in other shoal positions (see also Krause, 1993, 1994 for reviews of position-related costs and benefits). Note that the risk of the leading fish being eaten did not change with group size. Other group members, however, might benefit from a dilution effect as shoal size increased, even if predator success rate remained unchanged.

It has been reported that blue acara cichlids *Aequidens pulcher* (Gill), and pike *Esox lucius* L., prefer the larger of two fish shoals (within the ranges of shoal sizes tested in this study) on their first attack and spend more time attacking larger shoals (Krause & Godin, 1995; Krause, unpublished data). In theory, this could result in higher per capita risks for members of large shoals. However, the attack success of cichlids was correlated negatively with shoal size and a combination of attack rate and success showed clearly that fish in larger shoals were still safer. It is interesting to note in this context that rock bass did not exhibit any shoal size preference but always attacked the shoal that first came within attack range. It is possible that this was related to the nutritional state of the predator which was presumably hungry. However, there is also no particular reason why the bass should select for particular shoal sizes if they attack all sizes with about equal success. Thus the absence or presence of preferences for particular shoal sizes may well be linked to the hunting strategy used by the predator (the above cichlids were in full view of their prey and approached the fish shoals actively).

It is concluded that while hunting success of predators did not change with group size, per capita predation risk of prey may decrease with group size (as a result of risk dilution) but risk was not shared equally between group members with front fish being much more exposed to predation.

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