

GROUP VIGILANCE AND SHOAL SIZE IN A SMALL CHARACIN FISH

by

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Introduction

Animals living in groups may benefit from a reduction in individual risk of predation compared with solitary individuals (BERTRAM, 1978; PULLIAM & CARACO, 1984; GODIN, 1986). This can result from a number of antipredator mechanisms, including the greater probability that a group will detect an approaching predator than will a single individual (BERTRAM, 1978). This phenomenon has been termed 'early predator warning' (LAZARUS, 1979). Theoretically, the level of corporate vigilance increases at a decelerating rate with increasing group size (PULLIAM, 1973; TREISMAN, 1975; LAZARUS, 1979). However, early predator warning can only be an effective antipredator mechanism if information about the initial detection of the predator is socially transmitted among group members (TREISMAN, 1975; LAZARUS, 1979). Members of a social group can benefit further from their higher level of corporate vigilance and from information sharing in reducing their level of individual vigilance and, as a consequence, in allocating more time to other activities such as feeding (*e.g.* BARNARD, 1980; CARACO *et al.*, 1980; SULLIVAN, 1984; PITCHER, 1986).

Evidence that animals in groups detect predators sooner has been based largely on the positive correlation between flight reaction distance from an approaching predator and group size observed in several species

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(reviewed in YDENBERG & DILL, 1986). These latter studies have implicitly assumed that animals flee as soon as predators are detected. However, previous investigators have noted or shown empirically that a prey animal may not always flee as soon as it has 'detected' a predator (LAZARUS, 1979; SEGHERS, 1981; HANSON, 1984; GODIN & MORGAN, 1985; GODIN, 1986; YDENBERG & DILL, 1986). Therefore, any observed relationship between group size and flight distance in response to an approaching predator may not accurately reflect the perceptual ability of the group (*i.e.* group vigilance) as its membership changes (cf YDENBERG & DILL, 1986).

Fish schools and shoals (*sensu* PITCHER, 1986) provide considerable antipredator benefits to their individual members (GODIN, 1986; PITCHER, 1986). Fish in large shoals appear less timid, spend less time in cover and more time foraging than fish in small shoals (PITCHER, 1986), perhaps because fish in large shoals are likely to detect approaching predators sooner, and can consequently decrease individual vigilance and allocate more time to foraging (MAGURRAN *et al.*, 1985), as predicted by PULLIAM's (1973) model. However, an accurate description of the relationship between group size and vigilance, defined operationally as the probability that an individual will detect a given stimulus at a given time (DIMOND & LAZARUS, 1974), is lacking for fishes.

In the present study we quantify the relationship between shoal size and level of group vigilance in a strongly schooling characin fish, the glowlight tetra (*Hemigrammus erythrozonus*). Vigilance is here defined as the probability that an individual in a group will detect an artificial alarm stimulus at any instant in time. The relationship between shoal size and the number of individuals in the group responding (detecting) to the alarm stimulus was also determined. We then compare both these relationships with the ones predicted by a signal detection model described in TREISMAN (1975) and LAZARUS (1979). This model, based on the early predator warning hypothesis for social groups, predicts that group vigilance (as defined above) increases at a decelerating rate as a function of group size, but that the number of individuals in the group directly detecting the alarm stimulus increases linearly. Observed deviations from these predicted relationships would suggest that the model's assumptions (see details below) were violated, meaning that the probability of stimulus detection by any individual in the group was not independent of group size nor of the probabilities of detection of other group members. This would imply constraints limiting group vigilance as group membership changes, and also social transmission of information

(i.e. the alarm) among group members if the observed number of individuals in the group responding to the alarm stimulus exceeds the number expected. Our study therefore not only tests the predicted relationships of the aforementioned signal detection model, but also its underlying assumptions.

To accurately quantify these relationships, we constructed an apparatus designed to produce immediate fish fright responses to an alarm stimulus if detected. No rewards were provided to the fish in the apparatus, removing therefore any benefit of delaying their response. Further, the alarm stimulus suddenly appeared quite close to the fish (within 75 cm) and in a form which would be difficult to judge distance. Thus, no obvious advantage would accrue to the fish in deferring their response to the stimulus. A very brief underwater light flash was used as a sudden, novel alarm stimulus. Tetras react instantaneously to this stimulus with a Mauthner-driven startle acceleration (cf EATON & HACKETT, 1984), resembling the 'skittering' behaviour described by PITCHER (1986). Fish exposure to alarm stimuli which appear suddenly without warning in their visual field occurs in nature. For example, in structured habitats where piscivorous fish occur in close proximity to their prey (PITCHER, 1986), the latter commonly experience sudden, surprise attacks from ambush or stalking predators over very short distances, lasting only a few milliseconds (e.g. FOSTER, 1980). In such circumstances, the prey is expected to exhibit a flight response as soon as the predator is detected, because any delay in response would greatly increase the risk of being captured (ELLIS, 1982). Therefore, the occurrence of a startle (flight) response in the present study is interpreted as alarm stimulus detection and a measure of vigilance.

Materials and methods

Fish and holding conditions.

About 800 glowlight tetras ($\bar{x} \pm \text{SE} = 24.1 \pm 0.3$ mm total length; 0.17 ± 0.01 g wet weight; $N = 50$) were obtained from a local aquarium fish supplier. They were held in glass aquaria filled with aged well water, which was maintained at 21-23°C by immersion heaters and filtered by undergravel filters. The fish were fed several times daily with Tetramin flakes, a commercial dry fish food.

Experimental tank and apparatus.

The experimental tank consisted of two concentric rings of clear Plexiglas (30 cm high) glued to a white Plexiglas bottom (Fig. 1). The outside of the outer ring (100 cm diam.) was completely covered with black cardboard and the centrally located inner ring (50 cm diam.), which contained the test fish, remained transparent. The bottom of the zone between the two concentric rings was covered with a 0.5-cm layer of aquarium gravel,

whereas the bottom of the inner fish compartment was white. The tank was filled to 15 cm with aerated well water, which was maintained at $20.8 \pm 0.2^\circ\text{C}$. Overhead fluorescent lights uniformly illuminated the tank (900 lux, measured at the water surface in the centre of the tank). A video camera provided a top view from its location directly above the tank (Fig. 1). The entire apparatus was enclosed by a black polyethylene plastic blind to minimize fish disturbance.

Eight equidistant holes (3 cm diam.) were cut out of the black cardboard covering the outer wall of the tank 8 cm above the bottom; that is, about the middle of the water column. An incandescent white light source was mounted externally on each of these holes (Fig. 1), and each light source was connected separately to a remote timer. A very brief (1.0 s), low intensity light flash, which served as an artificial alarm stimulus (cf LAZARUS, 1979), could be presented to the test fish located in the central compartment from any of the eight peripheral light sources. Light intensity in the beam, measured underwater in the centre of the tank, was 3.4 lux or 0.4% of ambient light intensity. Therefore, the light flash was sufficiently bright and of high contrast against the black outer wall for fish to perceive it, but it did not raise ambient illumination enough to cast shadows of the fish on the opposing wall, thereby producing a secondary stimulus for response.

The test fish were confined to the central compartment, rather than allowed to swim over the entire tank, so that the chance of a single fish detecting a light stimulus was not so much dependent on its position in the tank but more on its orientation relative to the origin of the stimulus. Since the visual reaction field of fish extends mostly between 0 and 135° in the horizontal plane (LUECKE & O'BRIEN, 1981; DUNBRACK & DILL, 1984), the likelihood of a test fish detecting the alarm stimulus presumably decreases as it faces progressively further away from the point source of light.

Experimental procedure.

Glowlight tetras were tested separately as solitary fish and in groups of 2, 3, 5, 7, 10, 15, 20, 25 and 30 individuals, respectively. Prior to an experimental trial, an appropriate number of fish was selected, without known bias, from a holding tank and placed in the central compartment of the experimental tank. Following an acclimatizing period of at least 1 h, the fish were presented with a series of 10 novel light flash stimuli at 2-min intervals. At each interval, the stimulus light to be activated was determined at random from the eight available, so that its source was unpredictable to the fish and to reduce the likelihood of stimulus habituation. Changing the spatial context of a stimulus is known to prevent habituation of the response, or at least to reduce the rate of habituation (SHALTER, 1978; SCHLEIDT *et al.*, 1983). A tone was recorded on the audio channel of the video recorder at the same time as a light flash was presented; this tone served as a time marker during film analysis. Fish behaviour was filmed continuously from overhead during the course of the 20-min trial. The fish were not fed during the trial. At the end of a trial, test fish were placed in a holding tank separate from unused fish. Each trial was replicated 10 times for each shoal size. To avoid stimulus habituation between consecutive trials, no tetra was used in more than two different trials, which were at least two weeks apart.

From slow motion or frame-by-frame analysis of the films, the number of fish in the shoal exhibiting a startle response immediately (within 1.0 s) following the presentation of each of the 10 light stimuli during a trial was recorded and averaged for the trial. This number was then averaged over the 10 replicate trials, and normalized using the logarithmic transformation, for each shoal size. Fish behaviour was also observed during the 1.0-s period immediately prior to stimulus presentation (control period). Startle responses (*i.e.* false alarms) were never noted during this interval. The shoal was thus considered to have detected the light stimulus if at least one of its members exhibited a startle response immediately following stimulus presentation. Therefore, the probability of stimulus detection for each trial was calculated as the number of stimulus presentations

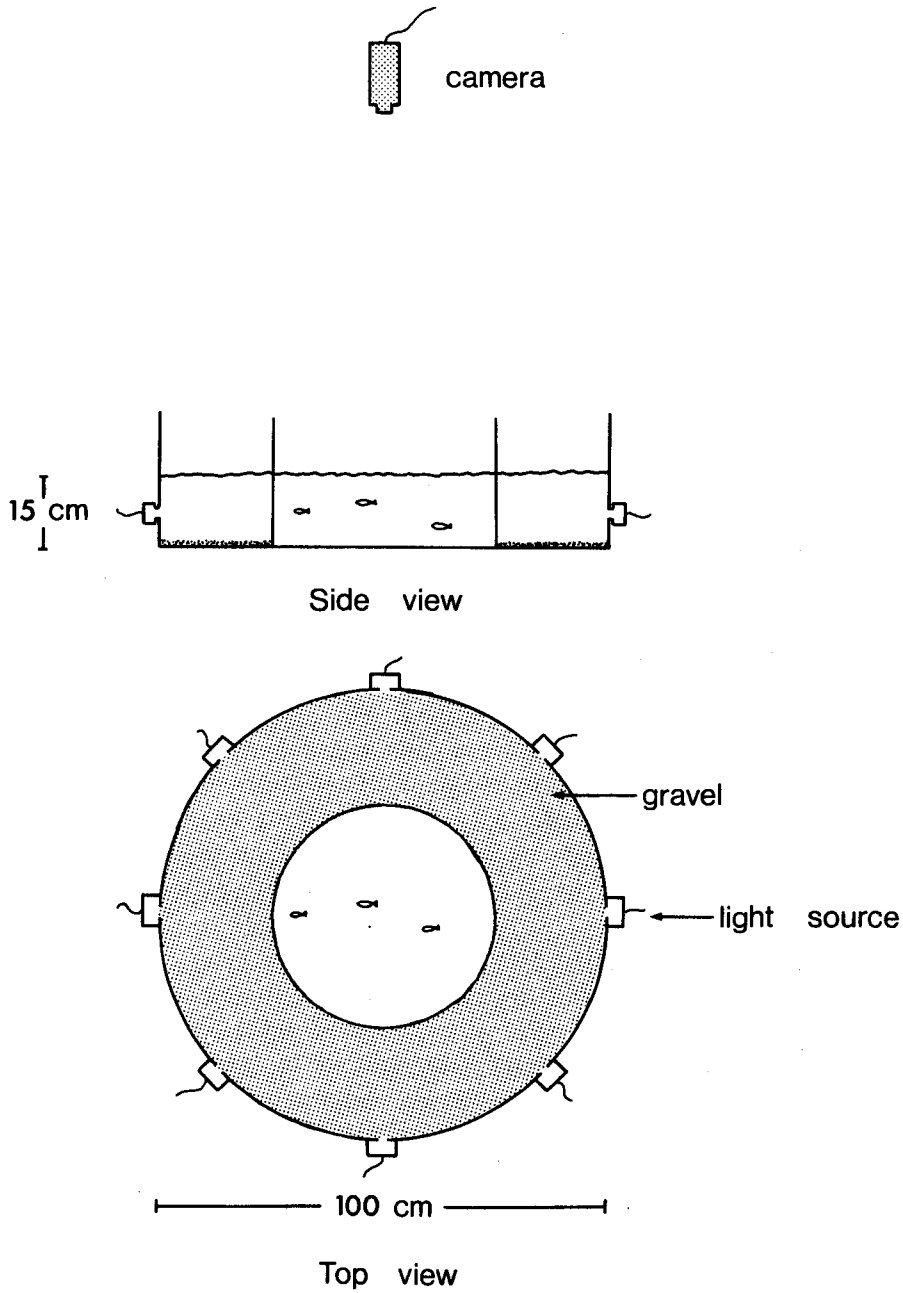


Fig. 1. Experimental Plexiglas tank with the central fish holding compartment, the eight peripheral stimulus lights and the overhead video camera shown. Further details are provided in the text.

out of 10 on which at least one fish responded, divided by 10. This proportion was then averaged over the 10 replicate trials, and normalized using the arcsine transformation, for each shoal size.

The observed probabilities of stimulus detection were compared with ones predicted by a signal detection model (TREISMAN, 1975; LAZARUS, 1979). The expected probability of detection, P_n , by at least one member of a group of size n is

$$P_n = 1 - (1 - P)^n, \quad (1)$$

where P is the probability of detection for a single individual. This model assumes that an individual's probability of detection, P , is independent of group size and of the probabilities of detection of other group members and that every animal is identical in its perceptual abilities. In the present study, P in equation (1) was taken to be the observed mean probability of detection for solitary fish (*i.e.*, $n = 1$). The expected number of fish responding in each group under the above assumptions is thus

$$nP \quad (2)$$

The expected standard errors of the mean for P_n and nP were calculated for each shoal size by inserting as P in equations 1 and 2, respectively, the standard error limits obtained for the observed mean probability of detection for solitary fish.

Results

Stimulus habituation.

To determine if the fish habituated to the stimulus lights during an experimental trial, we compared the frequency of startle responses exhibited on the first and last five stimulus presentations in the series over the 10 replicate trials for each shoal size separately. No significant difference in response frequency was noted for tetras in all shoal sizes tested ($p > 0.05$, Wilcoxon matched-pairs signed-ranks tests, two-tailed). Therefore, the fish apparently did not habituate to the stimulus lights. Consequently, a startle response is interpreted as signal detection and the absence of a response to the stimulus is not due to stimulus habituation.

Probability of stimulus detection.

The probability of stimulus detection increased significantly ($r = 0.78$, $F = 145.1$, $df = 3, 97$, $p < 0.001$) with increasing shoal size (Fig. 2). The relationship is curvilinear, with group vigilance increasing most rapidly between groups of 1 and 10 individuals. Although similar in form, the observed relationship between group vigilance and shoal size is just significantly different ($G = 17.02$, $df = 9$, $p < 0.05$, Log-likelihood ratio (G) goodness-of-fit test) from the one expected on the basis of the signal detection model presented earlier (Fig. 2). Since the expected values calculated using equation 1 (in Methods) are greater than most of the observed values (Fig. 2), one or more of the assumptions underlying this model were violated.

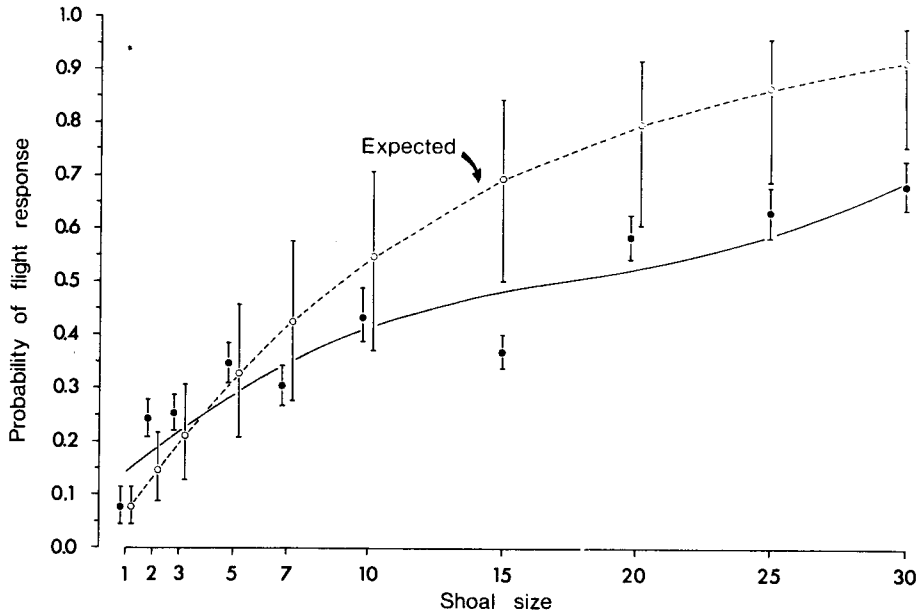


Fig. 2. Mean (\pm SE) probability of observing a startle (flight) response (*i.e.* probability of at least one fish detecting a single light stimulus) as a function of tetra shoal size. Each mean is based on arcsine transformed data obtained from 10 replicate trials. The observed relationship was obtained by a least-squares polynomial regression. The expected relationship was calculated using a signal detection model (equation 1 in text).

Number of fish in the group responding.

The number of tetras in a shoal exhibiting a startle response increased significantly ($r = 0.96$, $F = 1055.6$, $df = 2, 98$, $p < 0.001$) with increasing shoal size (Fig. 3). This relationship is significantly different ($G = 53.92$, $df = 9$, $p < 0.001$, G -test) from the one expected under the assumptions that an individual's probability of detection is independent of shoal size and of the probabilities of detection of other shoal members (Fig. 3). Greater observed values than expected in Fig. 3 indicate therefore that one or more tetras in the shoal responded directly to the light stimulus and other shoal members responded indirectly to the startle response of neighbours. The magnitude of the difference between observed and expected values increased with increasing shoal size (Fig. 3), and thus could be a measure of the extent of the social transmission of a flight response within the shoal. Additionally, we have carried out experiments which showed that individual tetras do not exhibit any observable response (including orienting reactions) to a 1-s light flash reflected off

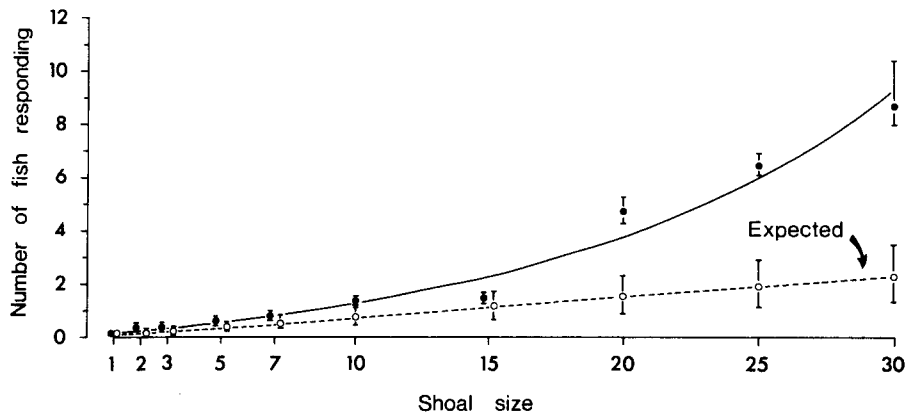


Fig. 3. Mean (\pm SE) number of tetras exhibiting a startle response to the stimulus light as a function of shoal size. Each mean is based on $\log_{10}(Y+1)$ transformed data obtained from 10 replicate trials. The observed relationship was obtained by a least-squares polynomial regression. The expected relationship was calculated on the basis of the signal detection model explained in the text (equation 2).

the body of a nearby conspecific. Consequently, observed startle responses in the present study resulted from either signal detection directly or indirectly in response to a fleeing neighbour.

Discussion

The present study demonstrated that corporate vigilance of a shoal of fish increases curvilinearly at a diminishing rate with increasing shoal size and that the flight response is socially transmitted among shoal members, particularly in larger shoals, as predicted by the hypothetical early warning function of group living (PULLIAM, 1973; TREISMAN, 1975; LAZARUS, 1979).

We have assumed that the presence of a startle (flight) response indicates stimulus detection and, more importantly, that the absence of such a response indicates failure to detect the alarm stimulus (cf Introduction). The effects of habituation on stimulus detection and the possibility of false alarm responses significantly contributing to the observed detection probabilities were ruled out. Therefore, the detection probabilities shown in Fig. 2 represent the corporate perceptual abilities of tetra shoals of different sizes. The form of the relationship between probability of detection and shoal size was one of diminishing returns, as predicted by equation 1. Although this relationship probably applies to

fish shoals in nature, the observed detection probabilities are particular to the test conditions and are probably unnaturally high, owing partly to the cryptic colouration of many fish predators, the complex underwater backgrounds against which they contrast and their diverse attack tactics (cf PITCHER, 1986).

The observed level of group vigilance increased most rapidly between shoal sizes of 1 and 10 individuals, and little change in group vigilance occurred with shoal sizes above 20 fish. Therefore, individual fish appear to gain little further antipredator benefit, through the enhanced predator detection ability of the group, as shoal membership exceeds 10 individuals. On the basis of this group vigilance pattern, one would expect individual risk of mortality to predation to decrease curvilinearly with increasing shoal size. Recently, MORGAN & GODIN (1985) reported such a relationship for shoaling banded killifish (*Fundulus diaphanus*) in the laboratory, where individual risk of predation decreased most rapidly in shoal sizes between 1 and 10 fish, above which little change in risk was observed. They attributed the latter relationship to the numerical dilution of attack rate per killifish in a shoal of a particular size and not to the enhanced predator detection ability of shoals, since the fish predator used in their study was always within view of the killifish. These two antipredator mechanisms are of course not mutually exclusive in nature.

If our assumption that stimulus detection was always followed by an observable startle response holds true, the discrepancy between the observed detection probabilities and those predicted by the signal detection model of TREISMAN (1975) and LAZARUS (1979) indicates that an individual's probability of stimulus detection was not independent of shoal size nor of the detection probabilities of other shoal members. Visual field overlap among group members can potentially increase with increasing group size in fishes (EGGERS, 1976), and could therefore constrain the level of group vigilance by restricting predator detection largely to individuals at the periphery of the group, especially in the larger ones (HANSON, 1984; GODIN & MORGAN, 1985). The level of vigilance of the group may be further limited by a corresponding reduction in the level of vigilance of individuals within the group with increasing group size, as observed in birds (BARNARD, 1980; CARACO *et al.*, 1980; SULLIVAN, 1984).

For individuals to benefit from the early predator warning function of group living, information about the initial detection of a putative predator must be socially transmitted among group members (TREISMAN, 1975; LAZARUS, 1979). The observation, that the numbers of tetras in a shoal

exhibiting a startle response exceeded those predicted under the assumptions of equation 1 (Fig. 3), suggests that social transmission of the flight response occurred within tetra shoals, and that the number of shoal members which responded indirectly to the alarm stimulus by reacting to the startle response of neighbours increased with increasing shoal size above 20 fish. Since individuals at the periphery of the shoal, and closest to the approaching predator, are more likely to detect the predator and to flee first (HANSON, 1984; GODIN & MORGAN, 1985), other shoal members gain an antipredator benefit by also initiating avoidance behaviour in response to the flight of the initial detector(s) (GODIN & MORGAN, 1985; GODIN, 1986). However, a potential cost of maximizing group vigilance and information sharing among group members by increasing group size is the chance of the group falsely 'concluding' that a predator is present when it is not and, as a consequence, wasting time and energy in fleeing. The likelihood of such false alarms occurring increases theoretically with increasing group size (TREISMAN, 1975). Another important factor which potentially selects against infinitely large groups is intragroup competition for limited resources such as food (BERTRAM, 1978; PULLIAM & CARACO, 1984; PITCHER, 1986).

Owing to the reduced individual risk of predation (GODIN, 1986; PITCHER, 1986), the enhanced corporate perceptual ability (this study; MAGURRAN *et al.*, 1985) and the increased foraging efficiency (PITCHER, 1986) associated with increasing shoal size, fish in large shoals can benefit more in delaying their escape from an approaching predator than solitary fish or fish in small shoals. This strategy would allow individuals in larger shoals to continue foraging for longer periods following predator detection, and (or) allow them more time to monitor the behaviour of the predator and to assess the nature of the threat (MAGURRAN *et al.*, 1985; PITCHER, 1986), which would reduce the frequency of costly false alarms (TREISMAN, 1975; LAZARUS, 1979).

Summary

The relationship between shoal size and group vigilance was investigated in the laboratory using a strongly schooling characin fish, the glowlight tetra (*Hemigrammus erythrozonus*). Group vigilance, as measured by the probability that at least one fish in the group detected (*i.e.* exhibited a startle response to) a brief, artificial alarm stimulus, increased curvilinearly at a decelerating rate with increasing shoal size. This would be predicted by the proposed early predator warning function of social groups. The observed relationship between corporate vigilance and shoal size was similar in form to one predicted by a simple signal detection model. However, observed detection probabilities for shoal sizes above 7 fish were lower than expected on the basis of this model, suggesting that an individual's probability of detection was not always independent of shoal size nor

of the probabilities of detection of other shoal members. The numbers of tetras in a shoal exhibiting a startle response to an alarm stimulus increased non-linearly with increasing shoal size and exceeded the values predicted by the above mentioned model for the larger shoals, which implies social transmission of the alarm response among shoal members.

The importance of the enhanced predator detection ability of fish shoals and the social transmission of alarms within them is discussed in relation to predator avoidance behaviour and other activities of fish in shoals.

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