

MORTALITY RISK OF SPATIAL POSITIONS IN ANIMAL GROUPS: THE DANGER OF BEING IN THE FRONT

by

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(Acc. 21-V-1997)

Summary

We modified Hamilton's (1971) selfish herd model by introducing directional movement to the prey groups and the predators. The consequences of this modification with regards to differential predation risks are compared to Hamilton's original model (using stationary prey groups) and tested against empirical data. In model 1, we replicated Hamilton's original predator-prey system. In models 2 and 3, prey groups were mobile and predators were mobile (model 2) or stationary (model 3). Our results indicate that additional to the positive risk gradient from centre to periphery predicted by Hamilton's model for stationary groups, there might be another positive risk gradient from the rear to the front part in moving groups. Furthermore, models 2 and 3 suggest that moving groups should generally exhibit an elongated shape (longer than wide along the axis of locomotion) if risk minimisation is the only factor concerned. Also smaller inter-individual distances are predicted for front individuals than individuals elsewhere in the group. Empirical data based on the three-dimensional structure of fish shoals (using roach, *Rutilus rutilus*) were consistent with the above two predictions. A second experiment which involved lake chub, *Semotilus atromaculatus*, as prey and rock bass, *Ambloplites rupestris*, as predators, provided direct support for the hypothesis that individuals in front positions of groups incurred a significantly higher predation risk than fish in rear positions. Finally, we discuss the differential

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⁶⁾ We are grateful to Dietmar Todt for providing us with facilities for the experimental part of this project and to Philip Muruthi and the members of the Ecology and Evolution Group of the Biology Department in Leeds for stimulating discussions. Helpful comments were also provided by William Hamilton and one anonymous referee. JK was supported by a BASF grant of the Studienstiftung des deutschen Volkes.

risks of different group positions in the context of potential foraging gains which provides the basis for a dynamic model of position preferences in group-living animals.

Introduction

Theoretical and empirical studies have shown that individuals in front positions of groups have a larger influence on the direction of group movements than ones in other group positions (Huth & Wissel, 1992; Bumann & Krause, 1993). Bumann & Krause (1993) suggested that front individuals are at higher risk than others because they are the first ones to enter new potentially dangerous areas whereas rear individuals follow in their 'footsteps'. The underlying idea of this concept is that predators attack the first prey that comes within striking distance as suggested by Hamilton (1971). Hamilton's (1971) selfish herd model addressed the case of a stationary prey group and a predator randomly located relative to the position of the group. His model showed that individuals in peripheral group positions should be at higher predation risk than those in the group centre — a prediction that was largely confirmed by empirical studies (Mooring & Hart, 1992; Krause, 1993a, 1994a; Krause & Tegeder, 1994). However, if we introduce directional movement to groups we should expect to find an additional negative risk gradient from the front to the rear of a group. We test this prediction by simulating three different predator-prey systems. The first one replicates Hamilton's model (for subsequent comparisons). The second model explores situations in which both prey group and predator move. And the third model considers the case in which only the prey group moves and the predator is stationary. The predation risk for individual group members in different group positions is calculated and compared for all three models. Based on the results of the simulations we derive two predictions for the structure of animal groups which we subsequently test against empirical data obtained from observations on fish shoals.

I. Simulation of predation events

We used computer simulation to calculate the *per capita* predation risk for stationary and moving prey groups each consisting of 100 individuals. For simplicity groups were assumed to be of circular shape and individuals

were randomly distributed within this circle (of radius x). In the first model, both the group and the predator were stationary. In the second model, both predator and prey group were mobile and in the final scenario, the group moved but the predator was stationary. In all three models, the starting position of the predator and its path (unless stationary) were random relative to the prey group's position and path. Predator and prey moved at equal velocity. In model 1, the predator attacked the nearest prey (*sensu* Hamilton, 1971). In models 2 and 3, the predator attacked the first prey that came within the attack distance of $x/2$ (variation of the attack distance from $0.1x$ to $1x$ showed that the precise numerical value of this distance was of little importance). The predator's starting co-ordinates were always outside a prey group (whereas in Hamilton's model, predators could also be located inside a group). Within prey groups all individuals moved at equal velocity and in the same direction. The *per capita* risk for group positions (front, rear, periphery and centre) were calculated from the number of attacks directed at individuals in an area divided by the number of group members in that area. For models 2 and 3, the group was divided into two equal halves which were defined as front and back halves relative to the direction of group movement. For the definition of periphery and centre, we divided the group into two concentric areas of equal size, an inner and an outer one. The radius of the smaller concentric circle was given as: radius = $(0.5x^2)^{1/2}$. Ten thousand predation events were simulated for each of the three models and the positions of the group members and the predator and the direction of the movements were independently generated for each event. All simulations were carried out for the 2-dimensional case.

Results and conclusions

In all three models, individuals on the periphery of the group were attacked more often than ones in the group centre (Fig. 1) (Binomial test, model 1, $N_1 = 9999$, $N_2 = 1$, $z = -100$, $p < 0.0001$; model 2, $N_1 = 9987$, $N_2 = 13$, $z = -100$, $p < 0.0001$; model 3, $N_1 = 9992$, $N_2 = 8$, $z = -100$, $p < 0.0001$). In model one (stationary prey group and predator), prey were attacked equally often in arbitrarily chosen front and rear halves (Binomial test, $N_1 = 4957$, $N_2 = 5043$, $z = -0.85$, $p = 0.4$). However, as movement was introduced to the prey groups, front individuals were significantly more often under attack than individuals in the rear (Binomial

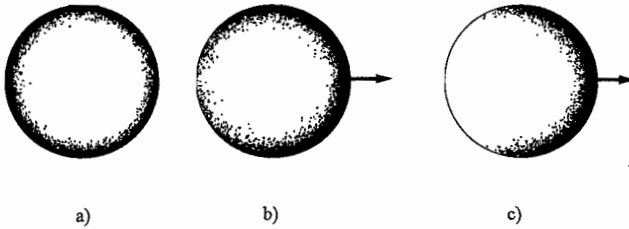


Fig. 1. Simulation of *per capita* predation risk (10 000 predation events per model) of a prey group of 100 individuals which are randomly distributed within a circular area defining the group shape. (a) Group and predator are stationary (*sensu* Hamilton, 1971). (b) Both the group and the predator continuously move with equal velocity. (c) Group moves and predator is stationary. The predator's starting position is random relative to the group position and the predator generally attacks the nearest prey. Black dots show the position of attacked group members for each case indicating which group positions were most vulnerable to predation.

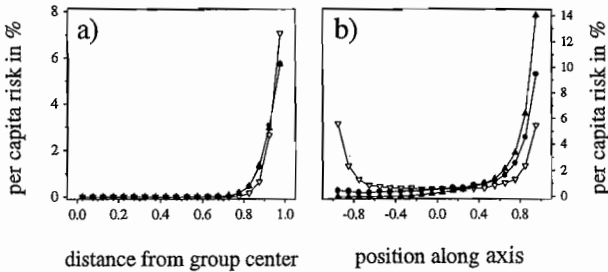


Fig. 2. Relationship between *per capita* predation risk and (a) the distance from the group centre and (b) the position along the axis of movement of the group (for the stationary group an arbitrary axis was chosen) for each of the three models. Negative values along the X-axis represent the rear part of a group and positive values the front part. Open triangles correspond to model 1, filled circles to model 2 and filled triangles to model 3.

test, $N_1 = 297$, $N_2 = 9703$, $z = -94$, $p < 0.0001$, Figs 1, 2). In the case of a stationary predator and a moving prey group (model 3), the *per capita* risk of individuals in the rear approximated zero and peaked for individuals in the front (Figs 1, 2). Model 2, in which both prey group and predator moved, represents an intermediate case in which individuals in the rear suffered a lower risk than front individuals but the difference was not as dramatic as in the model 3 (Binomial test, $N_1 = 1957$, $N_2 = 8043$, $z = -60.9$, $p < 0.0001$, Figs 1, 2).

In the following we will discuss models 2 and 3 in more detail. Front individuals were found to be at a considerably higher risk than other group

members which raises the question of what front individuals could do in a natural situation to reduce their risk: 1) they could change their position within the group either by decreasing their speed of locomotion (thereby being overtaken by individuals from behind) or by changing their direction of locomotion (turning around and back into the group); 2) they could move closer to their neighbours (thereby reducing their domain of danger, see Hamilton, 1971) which would result in smaller inter-individual distances; *i.e.* tighter spacing. Changing group positions (strategy 1) would lead to a breakdown of the group movement because none of the group members would stay up front whereas a reduction of inter-individual distances (strategy 2) would allow for a continuation of a directional movement of the group. Both of the above strategies can be observed in fish shoals: after encountering a strong fright stimulus, fish shoals often stop their directional movement and form stationary shoals of circular shape. In the absence of strong disturbances, however, fish shoals usually exhibit continuous sequences of directional locomotion (Krause, unpubl. data). It is important to note that front individuals could reduce their predation risk somewhat using strategy 2 but would still suffer a higher risk than their rear conspecifics. This higher risk might be at least partly be compensated for by other advantages exclusively associated with front positions — a point which will be taken up in the General discussion (see Krause *et al.*, 1992; Krause, 1994a; DeBlois & Rose, 1996).

In the following experimental part of this study, we focus on the case of undisturbed continuous group movement to test whether and to what extent strategy 2 is adopted by group members. We predict that front individuals should on average exhibit smaller inter-individual distances than ones in the rear of a group. Individuals in the middle and rear of groups should be able to reduce their risk by 'hiding' behind group members in front of them. This would lead to a lateral compression of the group. We should therefore expect the global shape of a moving group to be elongated (*i.e.* longer than wide, relative to the direction of locomotion). The above two predictions concerning the structure of moving groups are only made on the basis of differential predation risks for different group positions (see models 2 and 3) and do not necessarily apply when the group members are in a foraging situation (during which other group structures or even complete dispersal of the group may be favoured).

Hamilton's (1971) original model for stationary groups provided a potential explanation of the formation of groups and their coherence (once formed). Models 2 and 3 presented here suggest that the introduction of directional group movement leaves group coherence largely unaffected. The larger the extent to which rear individuals 'hide' behind the front fish, the more elongated the group structure. However, this is unlikely to break groups apart because rear individuals would then become front individuals and thereby experience a dramatic increase in predation risk.

II. Three-dimensional structure of fish shoals

Based on the previous section, we predict that the global shape of a moving group should be elongated and that individuals in the front part of a group should exhibit smaller inter-individual distances than group members in the rear part. In the following, we tested these two predictions using shoals of juvenile roach, *Rutilus rutilus*. Roach have a large number of different predators and spend most of their life in groups (Maitland & Campbell, 1992; Bumann & Krause, pers. obs.) which makes them suitable for an investigation of the relationship between shoal structure and predation risk. Furthermore, juvenile roach live in the littoral zone of lakes under conditions which can relatively easily be approximated in the laboratory (see Bumann & Krause, 1993).

Several hundred juvenile roach ($\bar{x} \pm \text{SD}$ standard length = 6.5 ± 0.5 cm) were collected from Lake Schlachten See (Berlin, Germany) and kept for several months in the test tank to acclimate them. Fish were fed TetraminTM flakes several times daily prior to testing. We used a light regime of 12L:12D and the water temperature was $20 \pm 1^\circ\text{C}$.

The test tank consisted of an inner area (2.6×1.3 m, 25 cm water depth) and an outer area (3×1.5 m). The tank walls were tilted so that the water depth gradually decreased between inner and outer zone from 25-0 cm. The fish preferred to stay in deeper water and avoided the tank periphery. Thus the gradual decrease in water depth minimised the effects of boundaries on fish shoaling behaviour due to their confinement in a relatively small area. The bottom of the tank and the walls were white to facilitate subsequent video analysis. Before each trial all fish were removed from the test tank and placed in a holding tank. Thirteen fish were randomly selected from the holding tank and re-introduced to the test tank. This procedure was used to make sure the fish were familiar with the interior of the test tank and therefore showed normal swimming phases in mid-water (timid fish stick to the tank bottom and hardly move). After 30 min acclimation all swimming phases within view of the cameras for more than 2 s were recorded. Sequence length was restricted by the camera angle of 1×0.8 m which was chosen to obtain sufficient resolution. Video recordings

were made with two cameras placed 0.8 m apart (see Bumann & Krause, 1993, for the details of the recording system) and digitised using a FG-100 board (Image Technology) attached to a PC. On every frame each fish was identified individually and its centre of mass calculated. The co-ordinates of both recordings were combined to obtain three-dimensional time-resolved co-ordinates for each fish (see O'Brien *et al.*, 1986). The time resolution was 40 ms and spatial resolution was 3 mm for all co-ordinates. Altogether six shoals each consisting of 13 roach were observed. The same fish were not used repeatedly in different trials.

We obtained 3-4 sequences of 2-8 s duration for each shoal giving us a total of 20 sequences. The data from these sequences were pooled for each shoal. To obtain the shape of the shoal, we determined, for each frame, the spatial dimensions of the shoal in three perpendicular dimensions (*i.e.* length along the axis of movement, width, and height). For each sequence, the average of all its frames was calculated. Fish 1-6 were defined as front fish and fish 8-13 were defined as rear fish, based on the average swimming direction of the whole shoal for each frame. For both the front and the rear half of the shoal all 3-dimensional inter-individual distances between pairs of individuals were calculated (giving a total of 15 distances for each half). This was done for each frame of a sequence to obtain median inter-individual distances for both front and rear fish.

Results and conclusions

Shoals were longer (in the direction of the movement) than wide ($N = 6$ shoals, $p < 0.016$, Sign test; Fig. 3). The median ratio of the width to length equalled 0.82 (quartiles = 0.71, 0.95). The vertical dimension of all shoals was much smaller than the horizontal one (median ratio height: length = 0.14, quartiles = 0.11, 0.17). The elongated shape of roach shoals is consistent with the prediction of our simulations that fish in the middle and rear part of the shoal should minimise predation risk by 'hiding' behind front fish (Fig. 3).

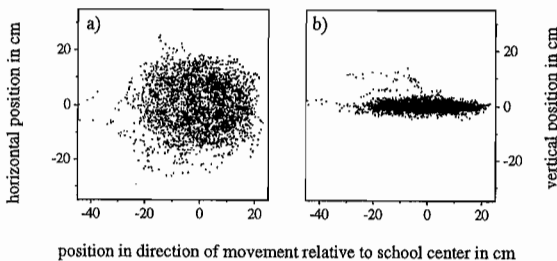


Fig. 3. Position of individual fish relative to the shoal centre. Measurements were taken every 200 ms and pooled for all 6 shoals giving a total of $N = 3640$ data points. (a) horizontal shoal positions and (b) vertical shoal positions.

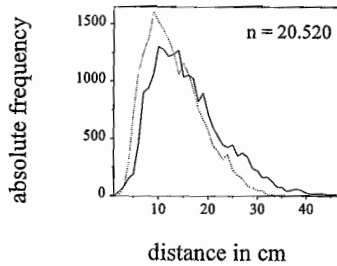


Fig. 4. Frequency of inter-individual distances compared for the front half (dotted line) and rear half (solid line) of the shoal. Data were pooled from all 20 sequences giving a total of 20 520 inter-individual distances.

The median inter-individual distance was significantly smaller for front fish than for rear fish ($N = 6$ shoals, $p < 0.016$, Sign test; Fig. 4). The reduced spacing of fish in front positions is consistent with our prediction that in moving groups, individuals in front positions should be at higher risk and therefore clump together more tightly.

III. Shoal position and predation risk

The following experiment was designed to test the prediction from model 3 (moving group and stationary predator) that individuals in the front half of a group are at a higher predation risk than ones in the rear half.

Several hundred creek chub, *Semotilus atromaculatus*, ($\bar{x} \pm SD$ standard length = 4.0 ± 0.1 cm) and 10 rock bass, *Ambloplites rupestris*, were caught from Stony Brook (Princeton, New Jersey, USA). Chub were kept in holding tanks at 15°C and fed *ad libitum* on TetraminTM flakes several times daily for several months before being used in the experiments. Bass were deprived of food for 24 h prior to the experiments.

Thirteen chub were taken randomly from the holding tank and introduced to the test pool (120 cm in diameter and 15 cm water depth; Fig. 5) using a transparent plastic cylinder. The chub were able to view their surroundings in the pool 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 Fig. 5). The hide consisted of a black floating plastic sheet (15×20 cm). The bass was introduced to the pool 24 h prior to the introduction of the prey fish and positioned itself inside the hide within a few seconds of introduction and always stayed there throughout a trial. Due to an inverted opaque bowl ($L \times W \times H$: $50 \times 25 \times 20$ 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 (Fig. 5). The rock bass was always well-hidden inside the black plastic folds and the chub did not

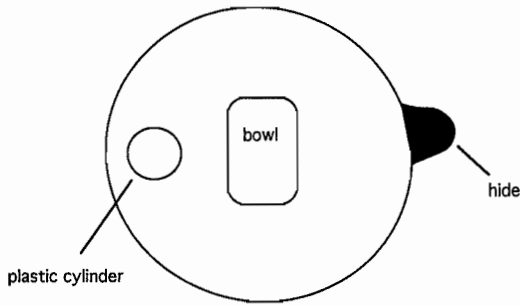


Fig. 5. Top-view of the predation experiments in section III. The bass was positioned in the hide. Prey fish were introduced on the opposite side of the tank (plastic cylinder) and did not have visual contact with the bass on release because of the opaque bowl.

avoid the hide or hesitate to approach. Thus there was no indication that they detected the bass before they were attacked by it. However, we cannot rule out the possibility that they sensed the presence of the bass through olfactory cues (Chivers & Smith, 1993).

The approach to the hide by the chub was recorded by a video camera from 1.5 m above the pool. Chub generally stayed very close to the pool bottom. Therefore a three-dimensional analysis of the shoal structure (based on recordings from two cameras) as in the previous experiment (section II) was not required. We recorded the shoal size, measured the attack distance (distance between the bass and the individual prey fish that was attacked) the outcome of the attack (successful or unsuccessful capture of a fish) and the shoal position of the fish that was attacked. Shoals sometimes split into subshoals before approaching the hide which is why shoal sizes (under attack by the bass) varied from 2 to 13 fish. A fish was considered to be in the front half of the shoal if it was in position 1 to $N/2$ (where N is the membership size) for shoals of even size and in position 1 to $(N - 1)/2$ for shoals of odd size. The bass attacked the shoal by launching out of its hide for a brief moment to which it immediately returned irrespective of whether the attack was successful or not. The bass did not pursue the shoals through the pool and we removed the shoal immediately after the first attack by the bass to minimise the stress for the prey fish. The bass never captured more than one single fish on a given attack and the shoal usually left the area quickly after the attack. Attack distance was estimated to the nearest centimetre from a grid on the bottom of the pool. The shoal position of an attacked individual was determined using the same criteria as in the preceding section (see section II). We carried out three trials with each of the ten bass giving us a total of 30 trials. However, statistical tests were only carried out using the first trial for each bass (to avoid pseudoreplication). Individual chub were not used repeatedly in different trials.

Results and conclusions

Nine fish was the average shoal size under attack by the bass and the average attack distance was 4 cm. The bass always attacked the closest fish. In 83% of the cases, this fish was also the leading fish of the shoal.

In all 30 cases, attacks were directed at an individual in the front half of the shoal resulting in a considerably higher predation risk for front fish (17 out of 30 attacks were successful). If we just consider the first trial for each bass, we obtain similar results: bass attacked the front half of the shoal significantly more often (Binomial test, $k = 0$, $N = 10$, $p < 0.001$) and given a capture, the probability for a fish in the front half to die was significantly higher than for fish in the rear half ($k = 0$, $N = 6$, $p < 0.016$).

Furthermore, our data indicate that the leading fish of a shoal incurred a much higher proportion of the risk than other shoal members. In 25 out of 30 cases, the leading fish was attacked and 56% of these fish were captured. Statistical analysis of these data is complicated by the fact that we cannot compute an expected probability of attack (across trials) for the leading position due to the variability in shoal size between trials (see above). This problem does not affect the above comparison between front and rear half of the shoal because those probabilities could be calculated independently of the actual shoal size.

General discussion

The original selfish-herd model by Hamilton (1971) showed a strong positive gradient in predation risk from the centre to the periphery of a group. The results presented here demonstrate that as we introduce movement to our models, we get an additional risk gradient from rear to front with front positions being at the highest risk. There are many predator-prey systems that conform to models 2 and 3. Some marine bird species (such as pelicans, puffins *etc.*) are known to search the surface waters until they chance upon a shoal of fish. In this case, we have predators that move around and encounter prey groups that move as well (model 2). Stationary predators such as pike which lounge at fish shoals from cover or lions that attack herds of ungulates from a hide could be seen as examples of model 3. However, hardly any conclusive data identifying dangerous group positions have been collected so far from the field (Krause, 1994a).

Both predictions concerning the elongated shape and tighter spacing in the front half of groups are consistent with our observations on fish shoals. This is remarkable because the shoals used in the experiments were relatively small (only 13 fish) and nevertheless showed already significant

differences between front and rear positions. We should expect that these differences (between front and rear) become even more pronounced with increasing group size.

An elongated group structure and dense packing in the front half can potentially be related to factors other than differential predation risk. The fact that front positions are often better in terms of foraging (theoretical work: Eggers, 1976; planktivorous fish species: Krause *et al.*, 1992; Krause, 1993b; DeBlois & Rose, 1996; grazing geese: Black *et al.*, 1992; see Krause, 1994a, for a review) might be responsible for a decrease in inter-individual distances due to food competition. However, this is unlikely because the front part of a group does not have a limited spatial dimension and, in theory, all members of a group could be in the front at the same time forming a phalanx. Furthermore there was no food in the test tank during our experiments. Therefore the observed dense spacing of front individuals in this study is not likely to be connected to foraging behaviour. Hydrodynamical effects are another factor that could potentially influence the structure of fish shoals. However, roach use the so called 'burst-and-coast' swimming style where periods with active tail beating are interrupted by coasting periods. It has been shown that the hydrodynamic effects of schooling are very weak for this swimming style (Fish *et al.*, 1991). An elongated group structure could also be brought about by different speeds of locomotion of individual group members (Gueron *et al.*, 1996). In mixed-species groups, some species travel faster than others and/or larger individuals leave smaller ones behind. The use of only one species and the fact that individuals were matched for body length probably excludes this possibility as an explanation of the results found in this study.

Theoretical models (Huth & Wissel, 1992) as well as empirical studies (Bumann & Krause, 1993) have supported the idea that front individuals lead the group and initiate new directions more often than rear individuals. Thus the fact that rear individuals follow the ones in front of them is consistent with our concept of an elongated moving group in which front individuals are the first ones to explore new areas (and may thereby be exposed to higher risks).

The experimental part of our study provides direct evidence for the prediction of model 3 (mobile prey group and stationary predator) that individ-

uals in the front are at a higher predation risk than individuals elsewhere in the shoal. In fact our data show that 83% of all attacks were directed at the leading individual of the shoal which translated into a very high predation risk (given that an attack on any shoal member was successful, the chance of that individual being the leading fish was 82%).

Despite the fact that individuals within shoals often differ in their competitive ability and physical strength (Pitcher *et al.*, 1986; Milinski & Parker, 1991; Krause, 1994b), hierarchical systems are uncommon in fish shoals (Pitcher & Parrish, 1993). This is probably due to the continuous mixing of individuals from different shoals which does not allow for the formation of stable hierarchies. However, in some mammal species such as baboons, social ranks within groups are well developed and often easily recognised by certain phenotypic characters (silver fur in high-ranking male baboons, for instance). Field studies of baboons have shown that the high ranking males are usually the ones that lead the group into new foraging areas and in the event of a predation threat, high ranking individuals take up the front line to face the predator (Hall & DeVore, 1965; Rhine & Westlund, 1981; Cheney & Wrangham, 1987; see also Janson, 1990a, b). Rhine & Westlund (1981) reported that dominant males were the most likely to lead a group to water holes where the probability of encountering predators is greatly increased. In the above cases, the positioning of individuals of differential vulnerability (dominant males being less vulnerable than females and juveniles) reflects the predation risk of different group positions very clearly.

Previous studies have shown that front positions in groups provide considerably better foraging opportunities than other shoal positions (O'Connell, 1972; Krause *et al.*, 1992; Krause, 1993b, c; 1994a; DeBlois & Rose, 1996). Therefore the higher predation risks of front positions might be balanced by foraging benefits because they give first access to resources encountered by the group. Whether or not individuals take up front positions should then depend on their nutritional state and the trade-off between predation risk and food intake (Krause, 1994a). This is supported by field observations which showed that food-deprived individuals preferably occupied front positions in fish shoals but returned to rear or central positions after feeding at high rates for a certain time period whereas satiated individuals did not show any significant position preferences (Krause, 1993b).

Individual fish might therefore continuously rotate shoal positions depending on their nutritional state (Krause, 1993c, 1994a; see also Romey, 1995, for data on whirligig beetles). Thus our models and empirical data presented here further support the notion of anonymous groups as functionally and structurally heterogeneous.

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