On prey grouping and predator confusion in artifical fish schools

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Abstract

In two simulation models the benefit of schooling under predatory pressure is investigated. It appears that if a predator cannot become confused by prey, grouping is seldom beneficial. If prey, however, can confuse a predator, schooling appears to protect prey under a whole range of parameters. Using an evolutionary approach we found that, in the case of a confusable predator, cohesive groups with a consistent forward movement evolve most frequently, but that milling stationary groups also prove to be effective. We suggest that the predator protection in moving and stationary groups rely on different mechanisms, among other things, on a kind of altruistic behaviour.

Introduction

Similar to herds or flocks of other animals many species of fish gather in shoals or schools[1] without the need for leaders or external cues. Instead, it is thought that the (local) interactions between the group members lead through processes of self-organisation(Camazine et al., 2001) to the evident group structure. The character of these local interactions has been the focus of many models, e.g. (Niwa, 1994; Huth and Wissel, 1992; Aoki, 1982). Conceptually these models are identical in that individual fish relate their orientation and speed to that of their neighbors according to a few behavioral rules which we will refer to as avoidance (of collisions), attraction (centering) and alignment (matching speed and orientation). As has been demonstrated by means of computer simulations these behavioral rules lead to schooling behavior which looks natural to the human observer. However, in these models the question of what the benefits are of school formation is not addressed.

Of the many studies of the advantages of schooling (Pitcher and Parrish, 1993) there are indications for foraging benefits (Street and Hart, 1985), hydrodynamic advantages (Svendsen et al., 2003) and anti-predator functions. Here we will concentrate on the anti-predator function of schools. We will study prey-survival in a model on direct benefits of schooling (Zheng et al., 2005; Nishimura, 2002) and in an evolutionary model (Oboshi et al., 2002).

Shoaling fish counter predator attacks in many ways, e.g. by evasion such as flash expansion or by early detection of attacking predators (Pitcher and Parrish, 1993). Whereas these strategies are active and direct reactions of the prey-fish to the presence of a predator or an ongoing attack, we will concentrate on two different effects, namely the effect of grouping itself (it may reduce the probability of being found by the predator) and of confusion of the predator.

Grouping may be advantageous because in water fish shoals are barely better detectable than individuals (Pitcher and Parrish, 1993). Therefore, when the visual range is low compared to the speed of the predators and the fish, the predator has a much lower chance of encountering a shoal (because of their low number) than encountering fish that swim independently (as there are many). Nevertheless, Treisman shows that grouping is only beneficial if the predator (once a shoal has been detected) can only eat a small number of individuals while the rest can flee (Treisman, 1975). Here, we will nevertheless investigate under which conditions shoals might successfully avoid predators. Confusion of a predator reduces the success of an attack of a predator (Pitcher and Parrish, 1993; Krause and Ruxton, 2002) due to a multitude of available targets. Correspondingly, the decision of the predator about which individual to attack has been shown to take a longer time for larger shoals (Landeau and Terborgh, 1986). The reason for this could be twofold – by overloading the visual system (Broadbent, 1965) or by the difficulty of choosing between equal targets, the so-called effect of ‘embarrassment of riches’.

Here we will study the effects of grouping and confusion strategies on prey survival both for schooling and ungrouped prey. In a first model we will show how the number of surviving fish depends on the speed of the predator, the time that is needed to consume a prey fish (handling time) and on whether the predator is confused by too many prey-items or not. Next we will present the behavioral strategies that evolve in prey in an evolutionary model.

It is important to note that in these two models prey cannot

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[1] Groups of fish that aggregate for social reasons are commonly referred to as shoals (Pitcher and Parrish, 1993). Schools are shoals that swim coordinated and synchronized.

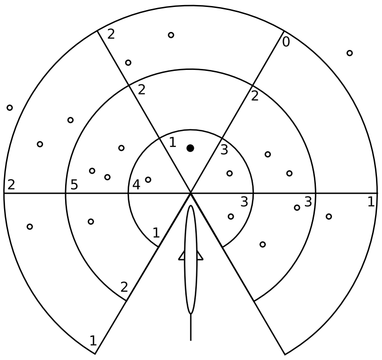

Figure 1: The sensory field of the predator is divided into five sectors that are subdivided in three areas. The crowdedness c_i (identical for all prey in an area) is the sum of the number of fish located in the same area and in the one immediately further away. The higher the crowdedness in an area, the better the protection for the prey due to the confusion effect.

parameter	direct effects	evolution	units
no. predators	1	1	
handling time	$0.2, 1.0, 1.8, 2.6, 3.4$	1.0	s
predator speed	$0.3, 0.6, 0.9$	0.6	$\frac{m}{s}$
number of prey	100	100	
prey behavior	schooling, ungrouped	evolved	
prey speed	0.3	0.3	$\frac{m}{s}$
sensory range[a]	5	5	m
blind angle[a]	60°	60°	
simulation time	100[b]	1000	s
runs	25[c]	3[c]	
size of arena	32 (torus)	32 (torus)	m

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[a] Identical for prey and predator

[b] Not including the time the predator is eating

[c] Random starting positions, agents in sensory range.

Table 1: Summary of the parameters used.

perceive the predator, therefore they cannot take any evasive action. This allows us to study the effects of grouping by prey and confusion of the predator independently from other anti-predator behaviours such as evasion and startling. We plan to incorporate evasion strategies in future work.

Methods

This section outlines the two types of prey agents used in the models and the predator, which is the same for both models.

At the start of each simulation, the prey and the predator were set at random positions with random orientation. The initial positions were confined to a limited area, in order that all the agents were in sensory range.

Predator

The predator agent needs to incorporate the two main effects we are interested in: Handling time and being confused.

Handling time. After the predator caught a fish, it stops for a certain time span, randomly changing its orientation. This reflects the process of consuming a prey.

Hunting behavior by confusable predator. To decide which prey to chase the predator assigns an "attractiveness" A_i^c for each prey in its sensory range.

$$A_i^c = \underset{\boxed{\text{distance factor}}}{\left(1-\frac{d_i}{d_{\text{view}}}\right)} \cdot \underset{\substack{\boxed{\text{confusion factor}} \\ (\text{if } c_i > 3)}}{\frac{0.5}{c_i^2}} \cdot \underset{\substack{\boxed{\text{prey locking}} \\ (i \text{ chased})}}{5} \qquad (1)$$

Firstly, the attractiveness A_i^c is a linear function of the distance d_i between predator and the prey i ($d_{view} = 5m$ is the sensory range of the predator). The closer a prey, the higher is its attractiveness. Secondly, to simulate confusion, this "distance factor" is multiplied with a "confusion factor" that reduces the attractivity. c_i (the "crowdedness" of the area where prey i is located) is calculated as indicated in Fig 1. For low values of crowdedness ($c_i \leq 3$) the confusion factor is omitted. Thirdly, if the prey i has been chased already in the last time step, it (rather unluckily) gets a bonus in the form of a "prey locking" factor of 5. This is to avoid that the predator keeps switching between prey in situations where several individuals have similar attractiveness. The predator then chases the prey with the highest attractiveness, given that it exceeds a certain threshold.

$$A_i^c > 0.1 \qquad (2)$$

Once the distance d_i of the chased prey to the predator becomes smaller than $0.1m$ the prey will be killed and eaten. If no prey with attractiveness above threshold is found, the predator moves straight ahead.

Hunting behavior by unconfusable predator. The architecture of the unconfusable predator is the same as that of the confusable one, but without the confusion factor.

$$A_i^u = \underset{\boxed{\text{distance factor}}}{\left(1-\frac{d_i}{d_{\text{view}}}\right)} \cdot \underset{\substack{\boxed{\text{prey locking}} \\ (i \text{ chased})}}{5} \qquad (3)$$

Of prey that are sufficiently attractive $A_i^u > 0.1$ the one with the highest attractivity is chased.

Model on direct effects: schools under predator attack.

Our first model uses a prey agent already developed for previous work. These agents are capable of schooling by the usual behaviour, namely turn away from neighbors which are too close, match the swimming direction to the average orientation of neighbors at intermediate distance and turn towards neighbors farther away (see (Kunz and Hemelrijk, 2003) for technical details). This model (of one predator and 100 prey agents) was used to investigate the benefits for grouping by prey for a range of parameters (handling time, predator speed) both for confusable and unconfusable predators. The parameters used are summarized in Table 1.

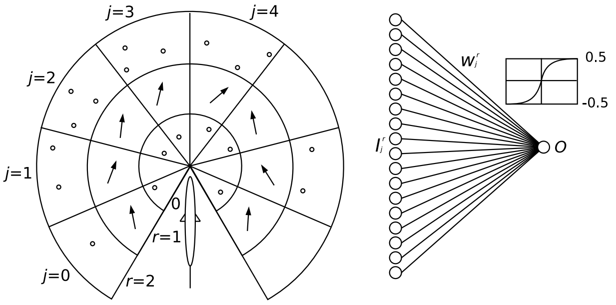

Figure 2: The sensory field of each agent is divided into eight sectors that are subdivided in three areas. A simple neural network is used for the sensory processing. Each input I_j^r node is assigned to an area of the sensory field. Not every area delivers the same information, though. Inputs located in the closest and outermost areas ($r = 0$ and $r = 2$) feed the number of agents (located in that area) into the neural network. Inputs in the intermediate areas ($r = 1$) provide the average relative orientation of the agents located in the respective areas.

Evolutionary model: prey under predatory pressure.

The second model uses an evolutionary approach with a different type of prey agent (see Fig. 2). The agent uses a simple neural network to control its movement. The inputs I_j^r are specified in Fig. 2. The output O of the network

$$O = f(\sum_{j=0}^{5}\sum_{r=0}^{2} w_j^r \cdot I_j^r), \quad f(x) = \frac{1}{1+e^{-x/1.5}} - 0.5 \qquad (4)$$

determines the turning angle

$$\phi = 2\pi O, \quad (\phi \text{ clipped to the interval } [-40^\circ, 40^\circ]) \qquad (5)$$

and thus the new velocity vector[2]

$$\angle \mathbf{v}^{t+\Delta t} = \angle \mathbf{v}^t + \phi, \quad \left\|\mathbf{v}^t\right\| = 0.3\tfrac{m}{s} \qquad (6)$$

and consequently the movement

$$\mathbf{x}^{t+\Delta t} = \mathbf{x}^t + \mathbf{v}^t \Delta t, \quad \Delta t = 0.2s \qquad (7)$$

Thus, the weights w_j^r in the neural network determine the prey behavior. Since only unbiased behavior is desired here (i.e. the reaction to neighbors to the left and to the right should be identical) the weights on the right-hand side are determined by the corresponding weights on the left.

The parameters of the predator were chosen deliberately such that grouping would be disadvantageous in the case of an unconfusable predator. For a summary of the used parameters see Table 1.

Since we use an evolutionary approach here, we leave it to a genetic algorithm[3] to find optimal weights for the prey to survive as long as possible. The set of weights therefore constitutes the genome.

The evolutionary algorithm is working on a group of identical prey agents (all have the same genome and thus the same neural network). The groups were evaluated by two criteria, namely the percentage of surviving agents and the ratio of collisions amongst prey agents,

$$\text{fitness} = \tfrac{n_{\text{alive}}}{n}\left(1 - \tfrac{n_{\text{collision}}}{n}\right) \qquad (8)$$

where $n = 100$ is the total number of prey agents (at the start of the simulation), n_{alive} is the number of prey agents still alive at the end of the simulation (after $1000s$) and $n_{collision}$ is the number of prey agents which are closer than $3cm$ to their nearest neighbor (measured at the end of the simulation).

A total of 25 evolutionary runs were simulated, in each of which a pool of 30 groups (of 100 individuals and 1 predator) were evolved for 100 generations. In each generation, for each of these 30 groups the fitness (see above) was evaluated.

At the end of a run the group with highest fitness was selected for analysis. Further, each time a prey was captured, its nearest neighbor distance and the average nearest neighbor distance were saved. Additionally, the degree of coordination (see below) was measured at the end of each run.

Statistical measurements Besides the number of surviving prey the following measures were calculated. To characterize the compactness, we used the average nearest neighbor distance. The degree of alignment is measured by the coordination (polarization) p defined as

$$p = \frac{1}{n}\sum_{i=1}^{n}\left(1 - \tfrac{|\angle(\mathbf{v}_i, \mathbf{v}_{avg})|}{\pi}\right)$$

where $\mathbf{v}_i$ is the velocity of prey i and $\mathbf{v}_{avg}$ is the average velocity over all prey agents. For perfectly coordinated groups we would get $p = 1.0$, for totally uncoordinated groups we would expect $p = 0.5$.

The degree of 'solitude' indicates the degree with which captured prey were exposed. It is calculated as the ratio of nearest neighbor distance of the captured prey to the average nearest neighbor distance in the group, averaged over all captured prey fish. A solitude of 2 implies that the distance between the captured prey and their nearest neighbor were on average two times larger than the average nearest neighbor distance over all agents. A high solitude thus indicates that the captured prey was isolated and thus not part of a group.

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[2] Prey agents have a constant speed of $0.3m/s$. $\angle\mathbf{v}$ denotes the orientation of the vector $\mathbf{v}$ and $\|\mathbf{v}\|$ its length.

[3] A standard genetic algorithm was used (Goldberg, 1989). Our implementation uses `galib`, an open source general purpose genetic algorithm library which can be found here: `lancet.mit.edu/ga/`.

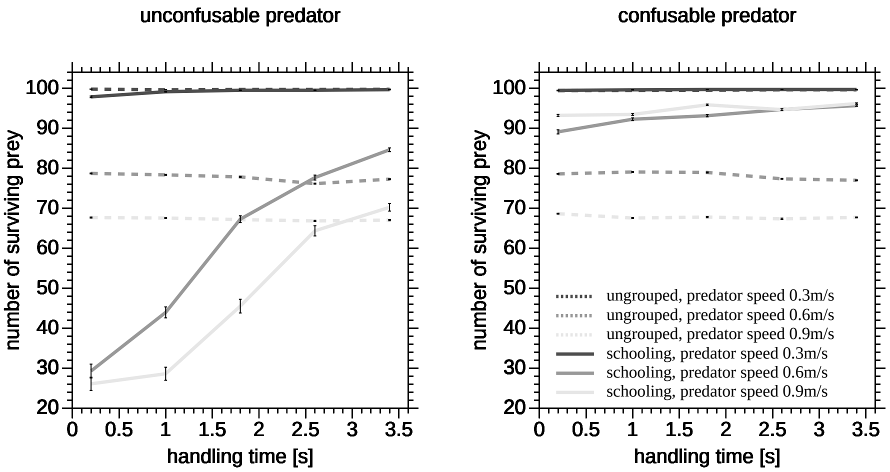

Figure 3: **Number of surviving prey.** The left panel shows the results of the simulations with an unconfusable predator, the panel on the right depicts the same situation for a confusable predator. Solid lines correspond to schooling prey, whereas dotted lines depict simulations where prey moves independently. The darkness represents the speed of the predator.

Results

Direct benefits of schooling

As is shown in Fig. 3 (left panel), the number of surviving prey in schools increases when it takes the unconfusable predator more time to handle and eat the prey (solid lines). In contrast, when prey agents are ungrouped, the number of surviving prey does not depend on the handling time. When comparing solid and dotted lines of the same color we can see for which handling time (and predator speed) schooling or independent movement is more advantageous. In fact, for the parameters tested here, the grouping strategy is advantageous only for a very long handling time: for a predator speed of $0.6m/s$ handling time should be higher than $\approx 2s$ and for a speed of $0.9m/s$ handling time should exceed $\approx 3s$.

As expected higher predator speed generally leads to more prey being eaten, both for schooling and non-schooling prey. If the predator has the same speed as the prey, it can hardly capture any of them, despite the fact that the prey does not take any evasive action.

On the other hand, for a confusable predator schooling is always advantageous, even when the predator can consume prey in almost no time (see 3, right panel). Note, however, that here we compared only two behavioral strategies, namely schooling and independent movement. There may even be better strategies which we did not test here, whereby individuals group only under certain conditions.

Evolved behavior

The hypothesis here was that a cohesive strategy should evolve among prey agents when under attack of a confusable predator. Remember, that the predator parameters (handling time and speed) were chosen deliberately that the grouping strategy would not work with an unconfusable predator.

strategy		**#**	**S**
schooling	cohesive, consistent forward movement, not necessarily well coordinated	11	80
milling	cohesive, forming a closed loop, stationary	5	82
oscillating	cohesive, agents move synchronously towards and away from the center of the group, stationary	4	78
compact	very dense, stationary or moving	3	69
swarming	cohesive, uncoordinated, stationary	2	62

Table 2: Summary of the evolved grouping strategies. # denotes the number of times the strategy has evolved as the most successful one. ’S’ denotes the average number of surviving prey per strategy. Each run started with 100 prey agents.

Indeed, in all the 25 evolutionary runs cohesive strategies proved to be the most successful ones. In none of these strategies were the prey agents moving independently. Nevertheless, the strategies were not identical, see Table 2 for a summary[4]. Notably, in almost half of the runs schooling evolved. Interestingly, the second most frequent strategy was milling[5], a behavior which can also be observed in nature. The next frequent behavior, which we called ‘oscillating’ (where the individuals synchronously approach the group center and the again move away from it repeatedly), is not observed in nature, still it leads to similar good re-

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[4] The different strategies were discriminated by a human observer.

[5] Although the average number of surviving prey was slightly higher for milling than for schooling, we do not consider this difference as statistically significant because of the low number of samples.

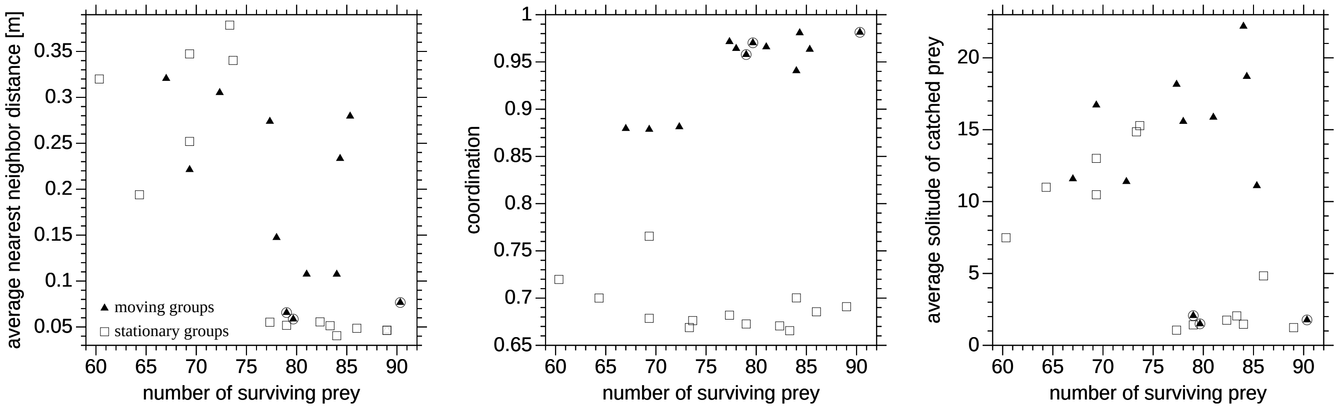

Figure 4: **Nearest neighbor distance**, **coordination** and **solitude** over the number of surviving prey. The squares correspond to stationary groups, the triangles to moving ones. The circled triangles denote moving groups with a different strategy. For details see the text.

sults as schooling and milling. Both the compact and the swarming strategies had a slightly lower number of surviving prey. Although, one would expect that compact groups would yield a better protection than less dense ones due to the confusion effect. The reason that the compact groups had a lower number of surviving prey can be explained by the observation that frequently individuals left the group, in one case the group dissolved entirely. Solitary prey is easily captured by the predator. The swarming groups had the lowest number of surviving prey, because of their low density at the periphery which reduced their protection by the group.

Nearest neighbor distance and coordination. We can get a more quantitative view of the evolved grouping strategies looking at average nearest neighbor distance and the degree of coordination. For both moving and stationary groups there seems to be a tendency that denser groups (with a lower average nearest neighbor distance) offer greater safety in terms of the confusion effect (see Fig. 4, left panel). Further, it seems that for stationary groups (red squares) the sheltering effect of dense groups is more important.

The importance of degree of coordination for survival is not immediate (see 4, middle panel). Obviously, the moving groups have a much higher coordination than the stationary ones (consistent forward movement requires a certain degree of coordination). Further, it seems that for stationary groups, coordination is of less importance. For the moving groups, on the other hand, a higher coordination indeed seems to correspond to a higher number of surviving prey. This could indicate, that for moving groups, the velocity[6] of the group is important.

Solitary agents. From the visual inspection of the simulations we knew that in many cases single agents left the group and were often chased (and eaten) by the predator. While bad for the individual, this behavior is potentially good for the group, as it distracts the predator from the group.

While this idea seems straightforward Fig. 4 (right panel) shows a more complicated picture. For the stationary groups it seems that such ‘altruistic’ behavior does not really help the group, as indicated by a low solitude for the groups with a number of surviving prey > 75 and lower numbers of surviving prey for the groups with a higher solitude. An explanation for this finding may be that solitary agents are captured quickly while the group is still in the sensory range of the predator (and can easily be attacked again). As the stationary groups cannot evade the predator (when the latter is handling a prey item) they have to rely on the confusion of the predator, which is reflected in small nearest neighbor distances (at least for the more successful groups, see also above).

In moving groups (especially in the more successful ones with number of surviving prey > 75) prey is often captured at a much larger distance from the group than for stationary groups. This means that in these cases solitary prey is captured by the predator, indicating that this ‘altruistic’ behavior of some prey agents is beneficial for the group. Indeed, as the group is moving it may evade the predator when the latter is chasing a solitary prey.

Note, however, that there are also highly successful moving groups where the solitude of captured prey is low (see circled triangles in Fig. 4). These groups are protected by confusing the predator because of their small nearest neighbor distance.

Discussion

In this study, the benefit of schooling (or cohesive behavior in general) under predatory pressure was investigated. Even though the prey agents could not perceive the predator (and thus they could not take any evasive action) it was still beneficial under a wide range of parameters to form groups.

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[6] As the velocity is strongly connected to coordination (Kunz and Hemelrijk, 2003).

In the model of direct effects of predation on schooling it appears that if a predator cannot become confused by prey, grouping is seldom beneficial. It is only advantageous if the handling time by the predator of the prey is long, so that the predator loses contact with the school while still eating its captured prey. Although predator speed has a strong effect on how many prey agents can escape from the predator, it does not greatly influence what the minimal handling time is under which schooling is beneficial.

If, however, a predator can be confused, schooling appears to be advantageous under a whole range of parameters, even if the predator handles each prey item very fast. This confirms that "the confusion effect is one of the most powerful forces that promote sociality in animals" (Landeau and Terborgh, 1986).

Next, an evolutionary approach was used to search for an optimal strategy. We found that in the case of a confusable predator cohesive groups with a consistent forward movement, i.e. schools, evolved most frequently. Although these groups had a considerable degree of coordination (otherwise they would be incapable of maintaining a forward movement) they lacked the high degree of coordination observed in real fish schools. Because it is possible to evolve highly coordinated behaviour using our prey model[7], the only explanation for the low degrees of coordination evolved here is that it is advantageous, because it causes single individuals to stray away from the group and these 'altruists' are more likely to be eaten and in this way help the group. We may hypothesize that strongly coordinated schools may evolve under slightly different circumstances, namely when a kind of energy minimization is involved (synchronized movement is considered to be more energy efficient) or when the prey agent can sense the predator and take evasive action (as synchronization is a strong mechanism to transfer information from one part of the group, were a predator has already been detected, to a different part, were the predator cannot be seen).

The second most frequent strategy that emerged was milling – a behavior which is also observed in real fish schools. This unexpected finding is interesting because milling, rather than being a "trap" for fish schools, appears to be beneficial as an anti-predatory strategy – at least in our experiments. Whether milling in real fish schools also serves as a protection against predators is, to our knowledge, an open question.

The third most frequent strategy that evolved we called 'oscillating'. This has not been observed in real fish schools, possibly because this behavior would be energy expensive.

Another strategy that emerged, which we called 'compact', has also been observed in real fish schools. Under predatory attack prey may form very densely packed groups, which makes it very difficult for the predator to single out individuals to attack (Hamilton, 1971).

The last strategy that evolved, namely swarming (or shoaling) is observed also in nature. Nevertheless, this strategy did not seem to be particularly effective in protecting the group against the predator.

When comparing stationary groups with moving ones in terms of average nearest neighbor distance and solitude, it seems that the predator protection may depend on two different mechanisms. Most of the more successful stationary groups are very dense ($nnd \approx 5cm$) and almost no prey agents leave the group. In contrast, for many (but not all) moving groups the nearest neighbor distance is much higher and a high fraction of the killed prey was captured outside of the group. For the few moving groups without solitary individuals nearest neighbor distances appears to be low. This suggests that the stationary groups and the moving groups without solitary individuals rely entirely on the protective effect of confusing the predator, whereas other moving groups employ a combined strategy, of on the one hand confusion and on the other hand avoidance by swimming away from the predator if it is busy chasing a prey that left the group.

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[7] Evidence for highly coordinated behavior was found in a separate set of evolutionary runs using the same prey model, but where the prey was explicitly selected for a high degree of coordination (data not published here).

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