

# Simulated Predator Attacks on Flocks: A Comparison of Tactics

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**Abstract** It is not exactly known why birds aggregate in coordinated flocks. The most common hypothesis proposes that the reason is protection from predators. Most of the currently developed examples of individual-based predator-prey models assume predators are attracted to the center of a highly coordinated flock. This proposed attraction of a predator to a flock would appear to be contradictory to an alternate hypothesis that flocks evolved as a protection against predation. In an attempt to resolve this apparent conflict, in this article we use a fuzzy individual-based model to study three attack tactics (attack center, attack nearest, attack isolated) and analyze the success of predation on two types of prey (social and individualistic). Our simulations revealed that social flocking (as opposed to individualistic behavior) is the optimal anti-predatory response to predators attacking mainly isolated individuals.

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## Keywords

Bird, flock, artificial life, boid, fuzzy logic, predator

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## I Introduction

The study of collective behavior is a fascinating field that analyzes how simple actions of an individual influence the complex global dynamics of a group. Aristotle once stated: “The whole is greater than the sum of its parts”—a statement that describes the essence of collective behavior. Typical examples of collective behavior are flocks of birds, schools of fish, and swarms of insects—phenomena that can be easily observed in nature. Collective behavior is also interesting because similar patterns emerge at smaller scales (cellular level) [6, 44].

Even though collective behavior is a common sight, it is still surrounded by mystery [27]. Several different hypotheses in the literature suggest reasons why animals sometimes coalesce into organized groups. The most common one proposes that such groups may function as an effective defense against predators [12, 22, 27, 37]. This hypothesis is supported by evidence that animals in groups may benefit from an increased probability of detecting a predator [9], individuals in groups may reduce the amount of time spent for predator vigilance [7, 42], and an individual in a large group may have a lower probability of being attacked by a predator [10]. Other hypotheses suggest that aggregating animals may benefit through higher mating efficiency, and more efficient foraging [23]. Some studies claim that fish schools or bird flocks save energy because of hydrodynamic or aerodynamic benefits [30]; however, the opinions on this matter are contradictory [3, 38, 48]. Our work focuses mainly on bird flocks; however,

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some of the results can also be applied to fish schools, since they have some similarities in structure and behavior, in that they both operate in a three-dimensional world [22].

Bird flocks are among the most widely observed, yet least understood, phenomena of collective behavior, mostly because of the difficulty of obtaining field data and, with the exception of a few types of urban flocks, the unpredictability of the appearance of highly organized flocks in nature [15]. Two types of highly organized bird flocks emerge in nature—cluster flocks, demonstrated by pigeons and starlings, and line flocks, such as can be seen in groups of geese flying in a vee [14]. Every evening, when birds that fly in organized groups return to their roosting areas, small flocks coalesce into giant cluster flocks, often numbering tens of thousands of birds. Birds may then perform complex aerial maneuvers before finally settling in their roosts [27]. Such behavior can often be seen every evening at the same place, so it might appear that birds flying in such flocks are actually attracting predators and making it easy for them to attack the flock, which runs counter to the idea that highly coordinated flocks evolved to reduce the impact of predation.

Complex flocking behavior can emerge if individuals follow simple rules. In 1987, Reynolds [41] published a ground-breaking article that presented the first computer flocking animation (*boids*). At the same time, Heppner and Grenander [16] were working on a similar project in which they modeled birds' behavior with stochastic nonlinear differential equations. In these two and most subsequent models, equations govern the behavior of the artificial animals (*animats*).

Our model uses fuzzy logic [51] and fuzzy-rule-based systems [5, 32], rather than equations, to develop the behavior of artificial animals.

Some current state-of-the-art models are in three dimensions and incorporate some simplified aerodynamics [17]. To make an in-depth study of shapes and patterns that emerge within the flock during a predator attack, a three-dimensional model would be required [13], but for the purpose of our study a two-dimensional model suffices, since some researchers suggest that the dimensionality of the model minimally affects the results of the simulations [18, 19, 24], and others believe that models should be as simple as possible [4].

Various authors have upgraded the basic models to add additional functionalities. Moškon et al., for example, used fuzzy logic to simulate the foraging behavior of artificial birds [33]. There are also several models that implement predators. All of them are based on Reynolds' model, and most of them use a predator that attacks the center of the flock [20, 29]. This tactic may be right for some species of real fish; a swordfish, for example, in nature typically attacks the center of a prey school. In the first attack it disperses the school, and in the following attacks it focuses on the individual fish that become separated from the rest of the group [45]. Compared to birds, however, fish may have better perception of the environment because of the lateral line, and schooling might be used to confuse the lateral line of predators [25]. Assuming that birds do not have a sense like the lateral line, avian predators in nature might not attack in such a fashion.

Others that studied predator-prey dynamics in collective behavior mostly focused on a flock's response to the predator's attack. For example, Inada et al. focused on common escape patterns that emerge [20], while Lee et al. analyzed how the size of the flocks changes during an attack [29].

In both cases the predator attacked the center of the flock. With respect to the hypothesis that flocks form as a defensive mechanism, targeting the center of the flock in hope of catching a prey might be viewed as a tactic based on pure luck. As already stated, this attack tactic might not be used by avian predators, except maybe for the first attacks, where the goal might be to disperse the prey in order to prepare for other tactics whose positive outcome was more probable. This research is not the first to propose different attack tactics; Nishimura [35, 36] was the first to study target selection mechanisms. The key differences between this research and Nishimura's studies are: (1) we use fuzzy logic; Nishimura used differential equations; (2) we model target selection through "realistic" visual perception; Nishimura expressed the probability of a prey becoming a target through a mathematical equation that does not take into account the position of the predator relative to the flock, nor its orientation; (3) in our model the prey that "sees" the predator tries to escape; in Nishimura's model it does not; and (4) we study social versus individualistic prey behavior; Nishimura studies ordered, partially disordered, and fully disordered prey motion.

According to Nishimura's study [36] the best predator tactic is to attack a peripheral target, and not an isolated target, as can be observed in nature [21, 45]. The reasons for this conclusion are two: (a) the equation Nishimura uses for a predator targeting isolated prey (Nishimura's strategy S) will not select any target if none exists that has a large enough separation from the flock; and (b) Nishimura's predator has perfect vision (i.e., it is able to perceive all prey), and it can happen that the predator will select a target that is on the opposite side of the flock and therefore requires a substantial amount of time to reach it. The first reason is unrealistic in that, of the three types of motion that Nishimura studies (ordered, partially disordered, and fully disordered), ordered motion, a rare event in nature, is a clear favorite. The second is unrealistic in that the selected target potentially might not be visible to the predator at all, due to occlusion.

The analysis of predator-prey pursuit is interesting not only from a biological perspective, but also from the perspective of control theory [34, 49]. The control theory approach could potentially represent an alternative, more mathematical approach to our study. However, we believe our fuzzy, individual-based model with its differences from Nishimura's approach permits a simulation whose behavior is closer to that of real birds.

## 2 Methods

The basis for our work is an existing fuzzy-logic-based bird flocking model made by Lebar Bajec et al. [28], called *synflocks*. An artificial animal, an animat, can be described using three qualities: (a) its *perception* of the environment, (b) its *drives*, and (c) its *action selection*. Perception acts as a filter for important information. Drives define desired actions that will fulfill the animal's needs. Action selection combines these actions and performs the appropriate locomotor response. Assuming the artificial universe consists only of artificial animals with no environmental factors like artificial trees, then an artificial animal's behavior is dependent mostly on the position, direction, and speed of the neighbors it perceives.

The animats in our model use the basic Reynolds drives—*cohesion*, *separation*, and *alignment* [41]. Cohesion simulates attraction toward flock-mates and is modeled as the animat's tendency to fly toward distant flock-mates when there are none nearby. Separation is a drive that helps the animats to avoid collisions—it forces an individual to fly away from flock-mates that are too close. With the third drive—alignment—animats coordinate their velocity (direction and speed of flight) with flock-mates. A visual representation of the drives can be seen in Figure 1. In our model the drives are described with simple linguistic if-then rules. Fuzzy logic is used for the transformation of the rules into numerical values: the desired change in direction and speed of each individual animat. More precisely, the if-then rules are used in a Mamdani fuzzy inference system [32] (see Appendix).

The original Reynolds model and most existing models are based on metric distance. In these models every animat within a limited radius influences the behavior of the observed animat; if an animat is outside that radius, it does not have any influence. Nevertheless, recent research [1, 2] suggests that in nature only around seven nearest neighbors influence an individual. As this technique is already gaining support in current state-of-the-art models [17], we likewise use a number-limited neighborhood (topological distance) instead of a radius-limited neighborhood (metric distance). In models based on topological distance, only a fixed number of nearest animats are influential, regardless of their distance.

Our model uses topological distance and concentrates on vision as the principal means of neighborhood perception. Our animat's field of vision is  $300^\circ$  wide, with a blind angle of  $60^\circ$  directly behind it. Most current models presume that birds have "perfect" vision and do not allow for the occlusion of distant birds due to other birds flying in the flock. Yet a recent study by Kunz et al. [24] shows that obstruction of vision increases the realism of simulations. Our model thus takes into account only seven visible (non-occluded) nearby animats (see Figure 1).

Predator and prey behaviors in our study are based on rules extracted from relevant theoretical literature and field observations. We modeled our simulations after a common scenario, where a

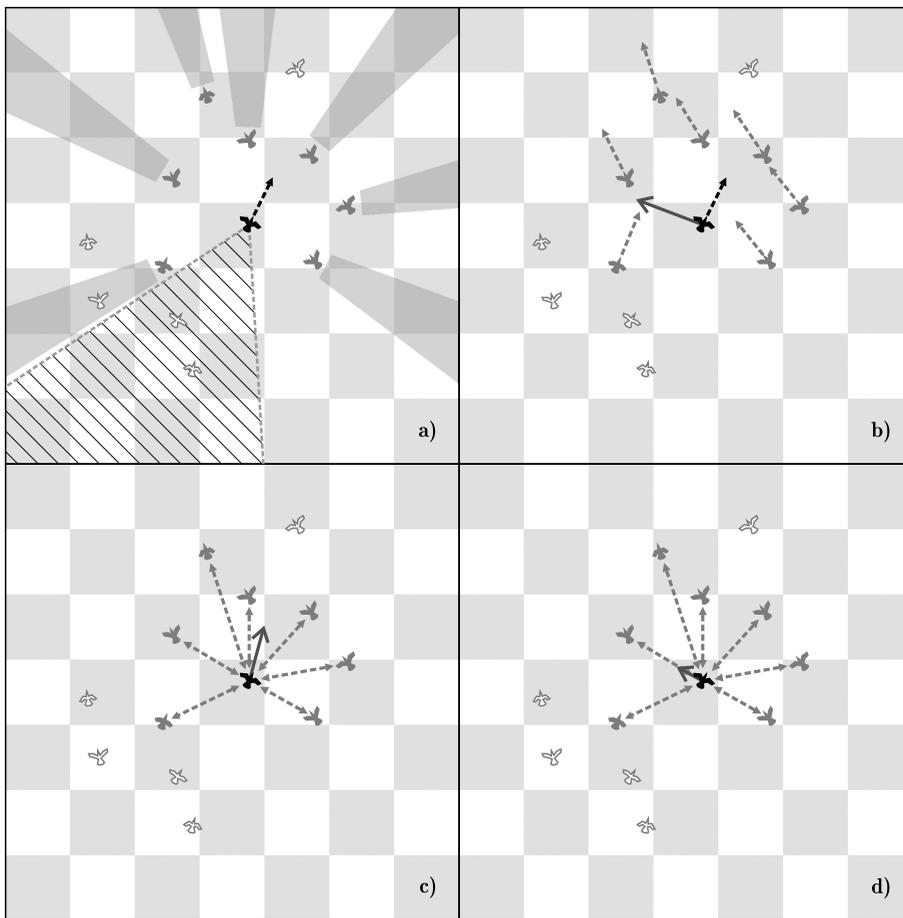


Figure 1. (a) Perception of nearby neighbors. The black bird is the observed individual. The dark gray birds are the perceived nearby birds that influence the observed bird's behavior. The white and outlined birds are either occluded by nearer birds (shaded areas), outside the observed bird's field of vision (hatched area), or outside the number-limited range. Red arrows represent the resulting force vectors of the three basic drives—(b) alignment, (c) cohesion, and (d) separation.

peregrine falcon (*Falco peregrinus*) is attacking a flock of European starlings (*Sturnus vulgaris*). In horizontal flight, the most economical flight speed (as to the amount of energy spent for flight propulsion) is around 60% of the bird's maximum speed [46]. Let us call this speed the *optimal cruising speed*. The optimal cruising speed of a European starling is 11 m/s, and the optimal cruising speed of a peregrine falcon is 13 m/s [46]. In accordance with these values we set the maximum speed of our prey animat to 18 m/s, and the maximum speed of our predator animat to 22 m/s. Note that we presumed that the peregrine falcon was not hunting by using its characteristic hunting stoop (high-speed dive), when it can reach speeds up to 157 m/s [47]. The minimum flight speed, in nature and in our model, is around 40% of the maximum flight speed [46], which amounts to 7.2 m/s for prey animats and 8.8 m/s for the predator animat. To define the predator-prey relationship we introduced three additional drives—*hide*, *seek*, and *regulate speed*. The prey's behavior is governed by the three basic drives (cohesion, separation, and alignment), and in addition *hide* and *regulate speed* (see Appendix for their explanation). The *hide* drive helps the prey to survive, as it forces it to fly away from the attacking predator; it was tuned so that the direction of the prey's escape matches field observations by Handegard et al. [11]. *Regulate speed* is only active when the *hide* drive is inactive—when the predator is hidden from the prey's sight. This drive encourages prey to fly with their optimal cruising speed. The

predator's behavior is guided only by the seek drive (see Appendix for its detailed explanation). With the seek drive the predator tries to catch the selected target.

We implemented three different attack tactics (see Figure 2). In our first tactic the predator attacks the center point of the seven perceived prey. This mimics the tactic in which a predator attacks the center of the flock in hope of hitting a target, but takes into account the limited amount of information available—distance, relative position, difference in speed, and difference in heading of the perceived artificial animals.

In the second tactic, the predator attacks the nearest of the seven perceived prey. The nearest prey might be the one that is also the fastest to reach, therefore making it a logical target for a predator. If a real predator chooses its prey in such a fashion, then flocking might work as a mechanism to reduce an individual's domain of danger [10]. The domain of danger is defined as the area in which the observed individual is the predator's nearest neighbor. Obviously, the average size of the domain of danger decreases if the number of birds in the flock increases, thus favoring tight, highly organized flocks. By reducing the domain of danger an individual lowers the probability of being attacked by the predator, thus possibly increasing its chances of survival.

A predator using the third tactic attacks the most isolated prey is the one that has the largest *angular distance* to its nearest neighbor. We define angular distance as the angle between a potential target and its nearest neighbor—from the predator's viewpoint. From a predator's viewpoint, isolated prey appear to have a large domain of danger because they are the most separated from the rest of the perceived prey. From the predator's perspective they would require the largest amount of time to decrease their domain of danger—time that is available to the predator to catch them. If we presume that flocking is indeed a protection mechanism, we can assume that the most isolated bird is the one that is the most vulnerable, making it a logical target for a predator.

### 3 Results and Discussion

To recapitulate, the predator in our model uses one of the following three attack tactics: (1) *attack center* (i.e., attack the center point of the seven perceived prey), (2) *attack nearest* (i.e., attack the nearest of the seven perceived prey), and (3) *attack isolated* (i.e., attack the most isolated, from the predator's point of view, of the seven perceived prey). In addition to escaping predator attacks and regulating their flight speed, the prey can exhibit two types of behavior: (1) *social* behavior (i.e., prey obey the cohesion, separation, and alignment drives) or (2) *individualistic* behavior (i.e., prey ignore the cohesion and alignment drives, but obey the separation drive to avoid collisions). In total this gives six combinations, through which we wished to answer the following questions: (1) what is the optimal

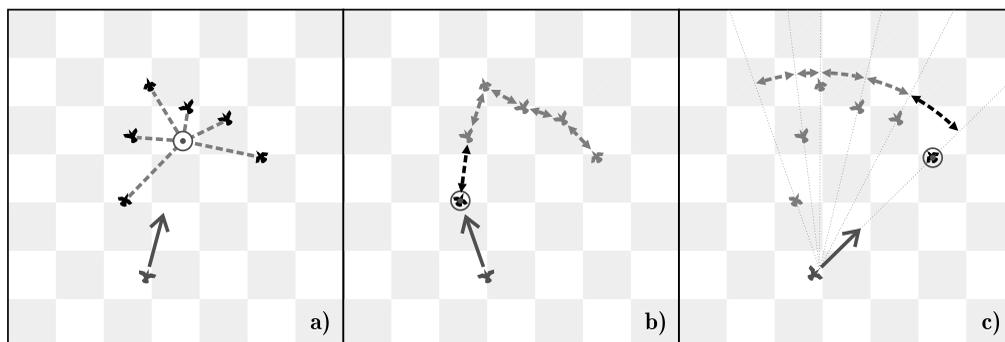


Figure 2. The three attack tactics: (a) the predator attacks the center of the seven perceived prey, (b) the predator attacks the nearest of the seven perceived prey, (c) the predator attacks the most isolated of the seven perceived prey. The red bird is the predator, and in the electronic version, the red arrow represents the resulting force vector of the predator's seek drive.

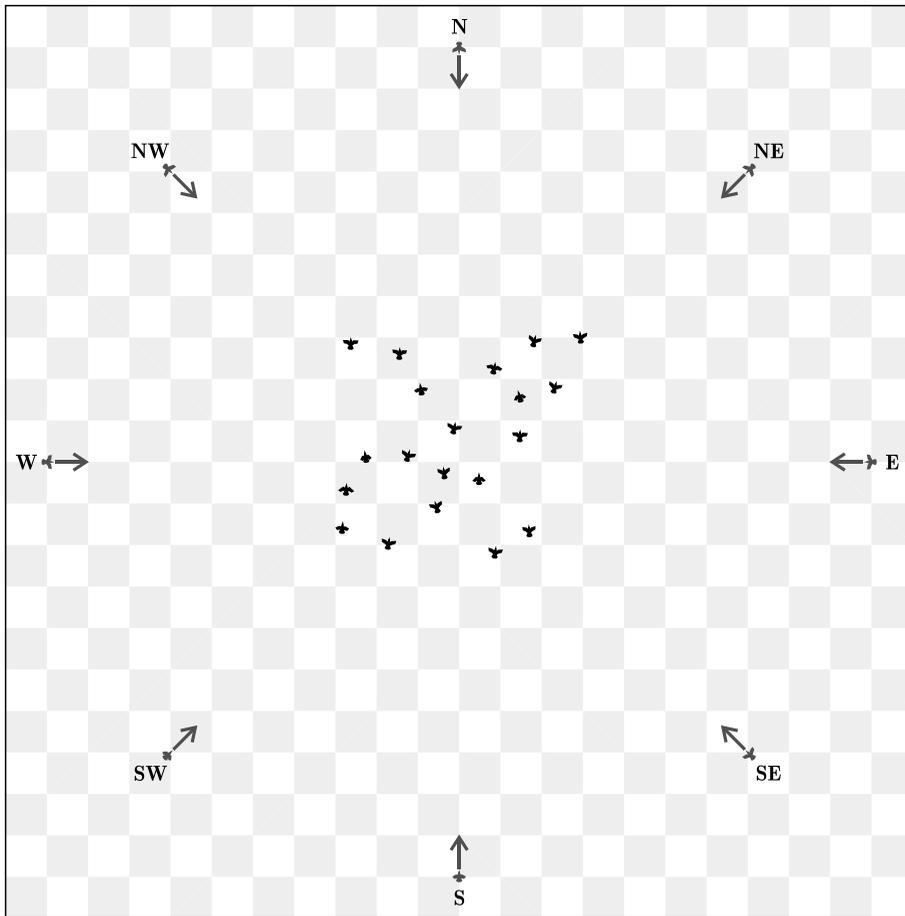


Figure 3. One of the starting configurations along with eight bearings of the predator's attack.

predator tactic, given a certain prey behavior, (2) what is the optimal prey behavior, given a certain predator tactic.

To provide answers to these questions we ran simulations where small cluster flocks consisting of 20, 40, or 60 social or individualistic prey were attacked by a predator from eight different bearings, relative to the flock. One of the starting configurations along with the eight bearings can be seen in Figure 3. The different bearings were used to eliminate any dependence of the simulation's results on the predator's bearing (e.g., a head-on attack versus an attack from behind). This gives a total of 432 simulations (72 per configuration, i.e., selected predator attack tactic and prey behavior). Each simulation was ran for 900 steps (frames)—30 s in our visualizations. We measured the time the predator needed to catch a prey. If the predator failed to catch the prey, the time to catch was set to 900 frames. The histograms of the time to catch for all simulations can be seen in Figure 4; a more in-depth discussion is given in the following sections.

### 3.1 Optimal Predator Tactic

Our simulations suggest that the best tactic for a predator attacking flocks of social prey is the attack isolated tactic ( $t = 3.01$ ,  $df = 142$ ,  $p = 0.003$ ). It would appear that isolated prey benefit the least from the advantages of flocking. On average the predator needed 279.74 frames (SD = 72.29) to catch an isolated prey. The predator whose tactic was to attack the nearest prey needed

316.74 frames (SD = 75.76) to catch its target, and the one whose tactic was attack the center of the seven perceived prey needed 845.08 frames (SD = 165.04).

With individualistic prey the best tactic for the predator is the attack-nearest tactic ( $t = 5.12$ ,  $df = 140$ ,  $p < 0.0001$ ). This finding makes sense, since the predator will get to the nearest prey faster than to those that are farther away. Predators that used this tactic needed, on average, 177.31 frames (SD = 33.95) to catch a prey. Predators that attacked isolated prey caught a prey in 208.06 frames (SD = 38.04). The attack-center tactic proved to be the worst, as the predator required 832.97 frames (SD = 198.89) to catch a prey.

The predator that used the attack-center tactic was, in most cases, not successful. In other words, it did not catch a prey in the 900 frames for which we ran the simulations (regardless of whether the prey was social or non-social). Thus the attack-center tactic proved to be the worst one, regardless of the prey's behavior.

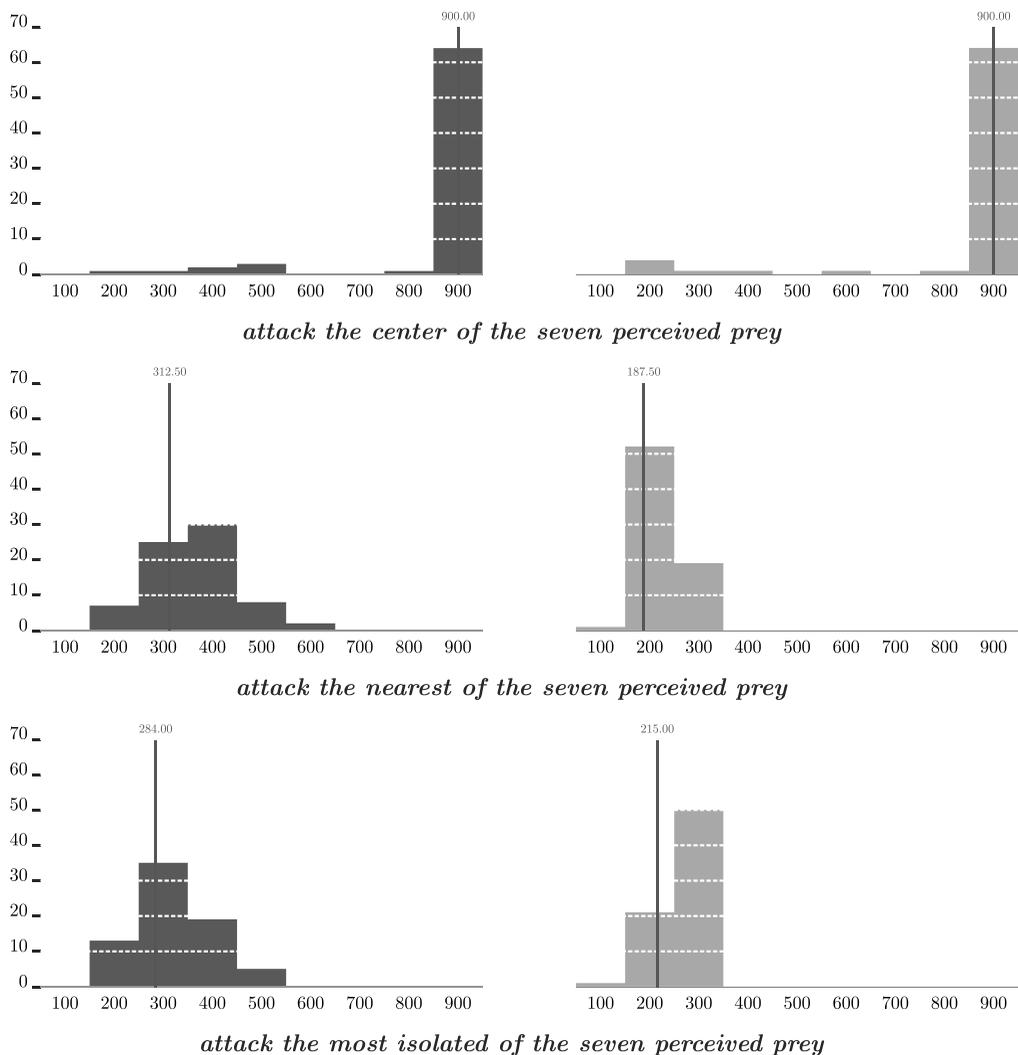


Figure 4. The influence of the predator's attack tactic and prey's behavior on survivability of prey. Presented are six histograms of the predator's time to catch in corresponding simulation runs ( $n = 72$ ). Dark gray histograms present the time to catch in simulations with social prey, whereas light gray histograms present the time to catch in simulations with individualistic prey (cohesion and alignment drives not used). In the electronic version, red lines present the corresponding median time to catch.

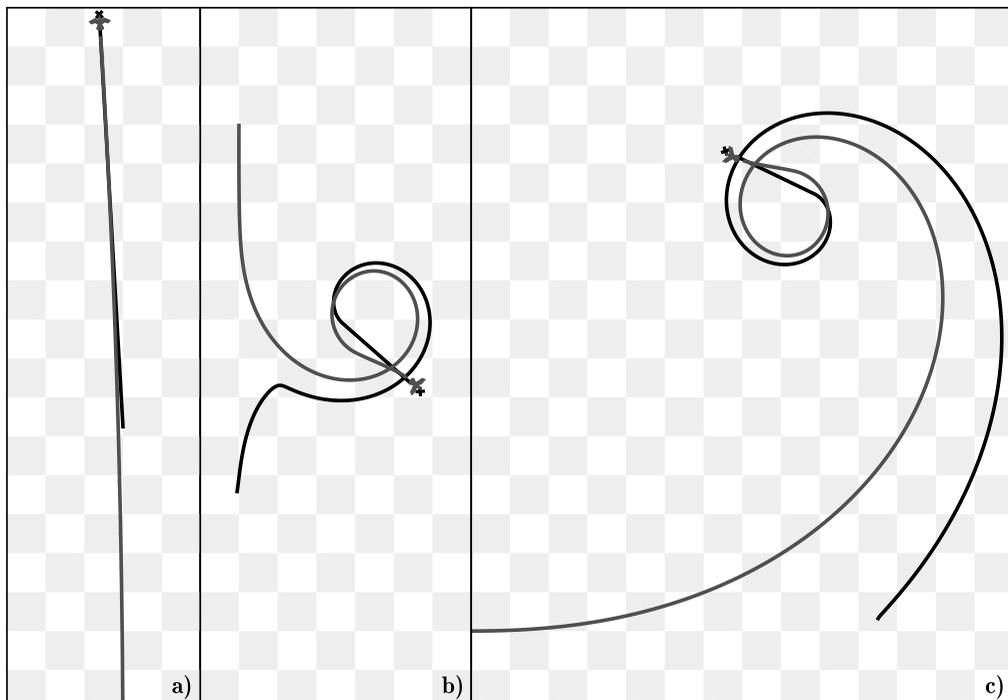


Figure 5. Predator attacking a single prey from three main directions: (a) behind, (b) head on, and (c) side.

As for the predator's best tactic overall, regardless of the prey's social or individualistic behavior, no difference was found between the two most successful tactics, attack nearest and attack isolated ( $t = 0.34$ ,  $df = 264$ ,  $p = 0.73$ ).

### 3.2 Optimal Prey Behavior

When the predator used the attack-center tactic, no difference was found for the average time to catch between social and individualistic prey ( $t = 0.39$ ,  $df = 137$ ,  $p = 0.69$ ). In both cases the predator was rarely successful, which is a direct result of the predator's tactic, which is based on pure luck.

With predators whose tactic actually tries to optimize the chance of a positive result, however, the average time to catch is longer when prey behavior is social than when it is individualistic—more so when the predator targets the nearest prey ( $t = 14.25$ ,  $df = 98$ ,  $p < 0.0001$ ) than when the predator uses the attack-isolated tactic ( $t = 7.42$ ,  $df = 108$ ,  $p < 0.0001$ ).

The best tactic for prey attacked by a predator appears to be social behavior.

### 3.3 Biological Relevance

Fine-scale sonar tracking of interactions among predatory fish and their schooling prey performed by Handegard et al. [11] suggests that the most successful predators attack from behind. In our simulations, when the predator attacked from the side or front, the prey always managed to escape the initial attack. The predator was successful in one of the successive attacks that occurred from behind. Attacks from behind appear to be much more successful than other strategies, as in some cases, when the predator attacked from behind, the predator's initial attack was already fruitful. An example of the corresponding chase and escape paths in the case of a single predator attacking a single prey is presented in Figure 5.

In 1983, Pitcher and Wyche [39] defined several escape patterns. In our simulations, when the predator attacks the center point of the seven perceived prey, prey show similar escape patterns to

those in nature and existing fish school models. Indeed, we managed to spot three of the escape patterns defined by Pitcher and Wyche [39]: *herd*, *split*, and *fountain*. The herd pattern can be seen at the beginning of a predator approach. The herd pattern then morphs into either split or fountain. Split occurs when a large flock is divided into smaller ones. A typical characteristic of the fountain pattern is that the split flock rejoins behind the predator. These patterns can be seen in Figure 6.

A more quantifiable measure was defined by Lee et al. [29], who defined three phases that can be seen in artificial flocks during a predator attack—*compression*, *expansion*, and *relaxation* (Figure 6). In the first phase of an attack the flock’s size decreases; this phase is called compression. In the second phase—expansion—prey try to move away from the predator. By doing this, the flock’s size increases. In the last, phase prey try to regroup, so the flock’s size again decreases. This last phase is called relaxation.

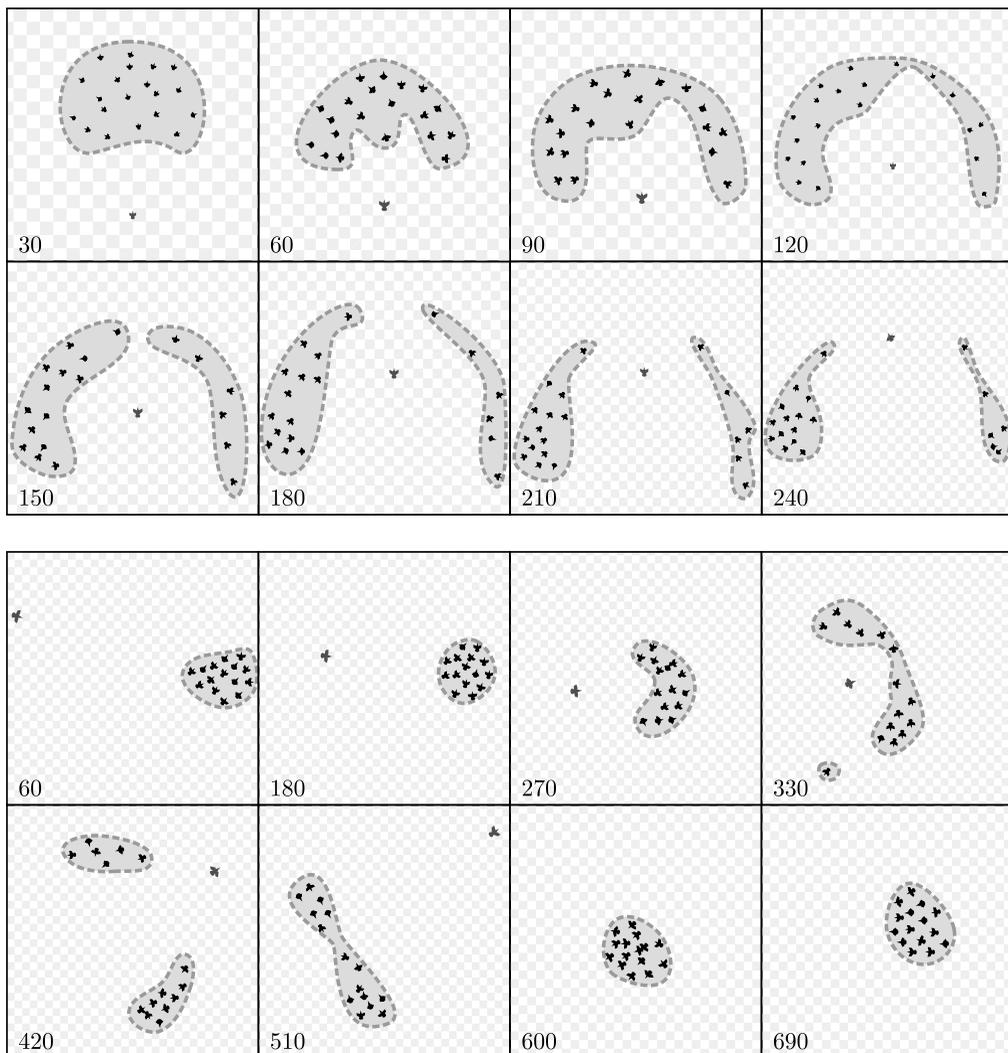


Figure 6. Three common patterns in the artificial flock’s response to a predator attack: (above) from *herd* (frames 30–120) to *split* (frames 120–240), (below) from *herd* (frames 60–330) to *fountain* (frames 330–510). In the snapshots below one can also notice the phases in the flock’s response: before attack (frame 60), *compression* (frames 60–180 and 510–600), *expansion* (frames 270–510), and *relaxation* (frames 600–690). In the electronic version, the red bird is the predator; black birds represent prey. For the sake of clarity the birds were scaled by 200% (above) and 300% (below).

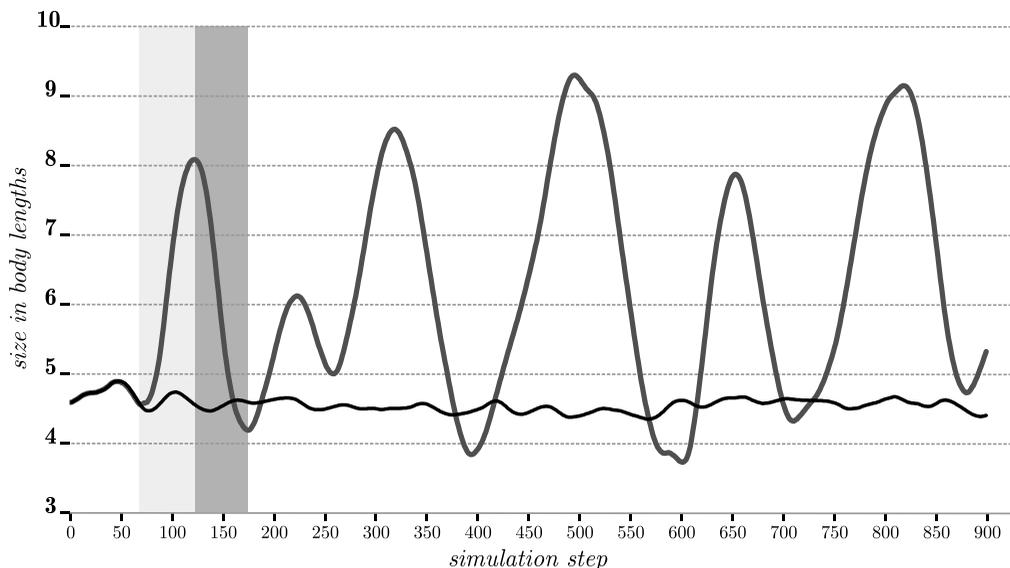


Figure 7. Plot of the flock size of an artificial flock consisting 20 animats. The black line shows the flock size over 900 simulation steps when there is no predator nearby. In the electronic version, the red line shows the flock size over 900 simulation steps when the flock is under predator attack. A clear example of flock expansion is marked with a light gray background, and dark gray is used to mark an example of flock compression. As predator attacks occur one after the other, there is no clear example of flock relaxation.

The three phases can easily be observed by tracing the artificial flock’s *flock size*, as defined by Lee et al. [29]:

$$\sigma = \frac{\sqrt{\sum_{i=1}^N r_i^2}}{N}, \tag{1}$$

where  $r_i$  is the distance from the center of the flock to the  $i$ th individual, and  $N$  is the total number of animats in the flock. All of our simulations showed a similar response of the artificial flock to a predator’s attack. Figure 7 visualizes how, in our simulations, the flock size changes through time, both when the artificial flock is under threat from the predator and when there is no predator nearby. The flock size is measured in body lengths; one body length equals 20 cm, which is the size of a European starling.

#### 4 Conclusion

Our simulations show that the least successful predator is the one that attacks the center of the flock. They suggest that with predators whose tactic tries to optimize the chance of a positive outcome, social behavior is more advantageous than individualistic behavior, which strengthens our belief in the hypothesis that cluster flocking can be a mechanism for protection from predators.

The behavior of our artificial flocks appears to be comparable with that seen in flocks in nature. The average distance from the nearest neighbor is around four body lengths (one body length equals 20 cm) [2, 31, 40]; the response of an artificial flock to a predator attack is similar to field observations [29], and similar escape patterns to those in nature emerge [39]. Our results also show that the most successful predators attack from behind [11] and seek isolated targets [21].

Our results seem to suggest that cluster flocking around a roost is paradoxical, because although its structure might provide some protection against a predator attack, its very existence invites a

predator attack, and (at least in nature) there are always isolated individuals that can be picked off. It suggests also that at least in some circumstances, which may or may not be common in nature, tight cluster flocking can be of benefit to the flock as a whole, although it does not provide absolute protection to individuals in the flock.

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## Appendix: Supplementary Material

In our model the animat is defined as a three-stage process [26]: perception, drives, and action selection. For each animat the perception stage extrapolates data about the universe (other animats) that is available to the observed animat. In the drives stage, based on these data, a set of actions is computed that would fulfill individual needs of the modeled artificial animal. The action selection stage merges the actions and executes the locomotor response, thus changing the state of the universe.

### A.1 Perception

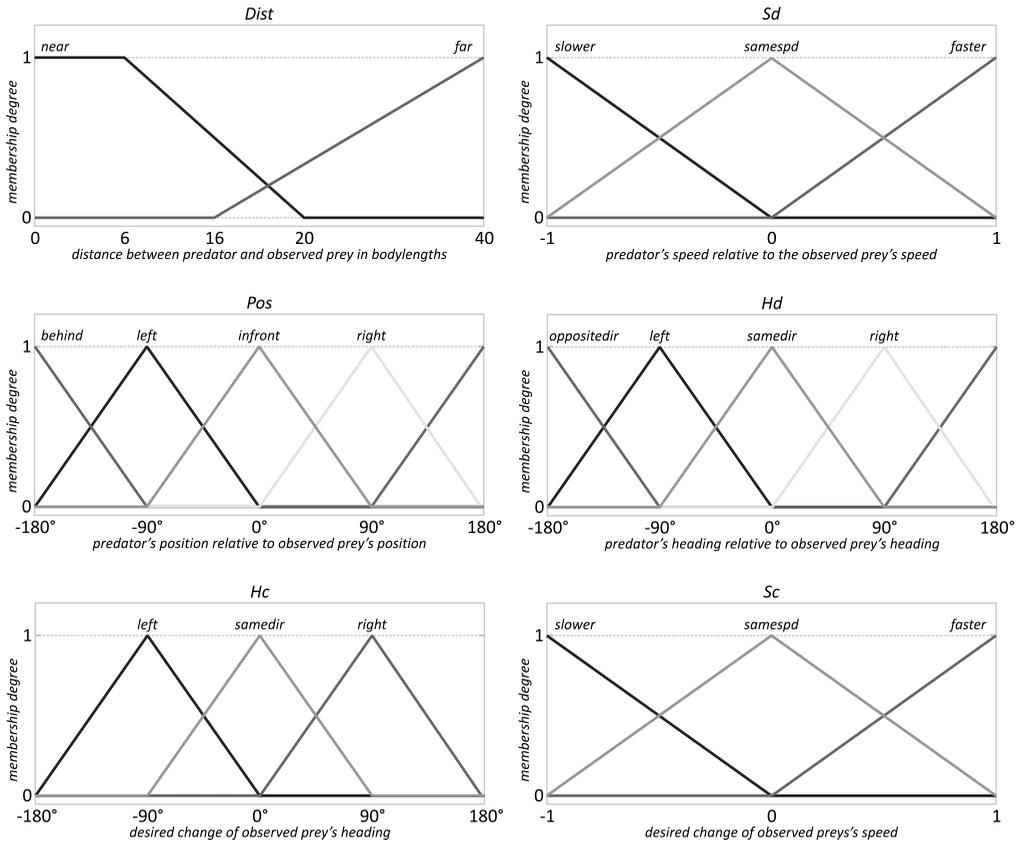
In our model the universe consists of animats only; the universe is in essence a list of animats. To extrapolate data about the universe, as a first step, the observed animat is removed from this list, and the animats remaining in the list are sorted based on their distance from the observed animat. Animats hidden by those that are closer to the observed animat and ones that are outside its field of view are then filtered out. The nearest seven animats remaining in the list provide the data about the universe. Only information about the relative position (i.e., angular offset with respect to the observed animat’s heading), distance, speed difference, and heading difference is passed on to the next stage.

Our approach differs from other existing models of number-limited neighborhoods (topological distance) [1] in that it always takes into account a fixed number of nearest neighbors. Other models typically implement the number-limited neighborhood as a *variable* radius-limited neighborhood [13]. In a variable radius-limited neighborhood, the observed animat will increase its radius of perception if in the previous step it perceived less than the specified number of animats, and decrease it if in the previous step it perceived more than the specified number of animats. This approach in truth varies the number of perceived animats in every step of the simulation, but limits it to the specified number. The principal reason this approach is taken is probably the speed of computation. Its drawback is that the observed animat could potentially perceive all of the other animats, provided these were distributed so that they were all at the same distance from the observed animat.

The number of objects that can be stored in working memory in humans and other mammals is small (four to seven) [1, 8]. The *hippocampus*, the structure in the brain primarily responsible for working memory, is generally similar in birds and mammals [43]. Our use of seven nearest animats in the perceptual world of the prey and predator is thus based on research on working memory. In addition, once the predator selects its target, in our model, it filters out all other potential prey, mimicking selective attention [50].

## A.2 Drives

The drives that result in actions that would fulfill the animat’s individual needs are modeled using Mamdani fuzzy rules [32]. For a detailed description of the cohesion, separation, and alignment drives, as well as a brief explanation of how a specific action is computed, the reader is invited to refer to [28]. An in-depth description is available in [26].

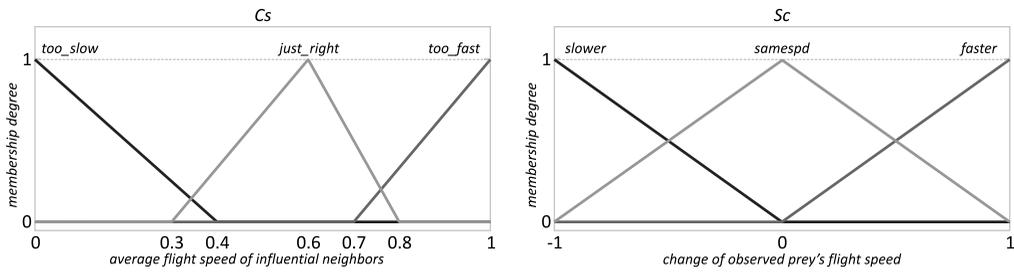


**Rules:**

```

if (Dist is near) and (Pos is left) and (Hd is left) then (Hc is samedir)
if (Dist is near) and (Pos is left) and (Hd is right) then (Hc is right)
if (Dist is near) and (Pos is left) and (Hd is samedir) then (Hc is right)
if (Dist is near) and (Pos is left) and (Hd is oppositedir) then (Hc is right)
if (Dist is near) and (Pos is right) and (Hd is right) then (Hc is samedir)
if (Dist is near) and (Pos is right) and (Hd is left) then (Hc is left)
if (Dist is near) and (Pos is right) and (Hd is samedir) then (Hc is left)
if (Dist is near) and (Pos is right) and (Hd is oppositedir) then (Hc is left)
if (Dist is near) and (Pos is infront) and (Hd is left) then (Hc is right)
if (Dist is near) and (Pos is infront) and (Hd is right) then (Hc is left)
if (Dist is near) and (Pos is behind) and (Hd is right) then (Hc is left)
if (Dist is near) and (Pos is behind) and (Hd is left) then (Hc is right)
if (Dist is near) then (Sc is faster)
if (Dist is far) then (Sc is samedir)
if (Dist is far) then (Hc is samedir)
    
```

Figure 8. Detailed description of the hide drive. On the membership function charts that describe speed, the value 1 represents the appropriate maximum speed (predator’s or prey’s), while -1 represents the negative value of the appropriate maximum speed. While these are the desired changes in speed, the action selection stage ensures that the current speed of the observed individual never falls below the appropriate minimum speed (predator’s or prey’s).



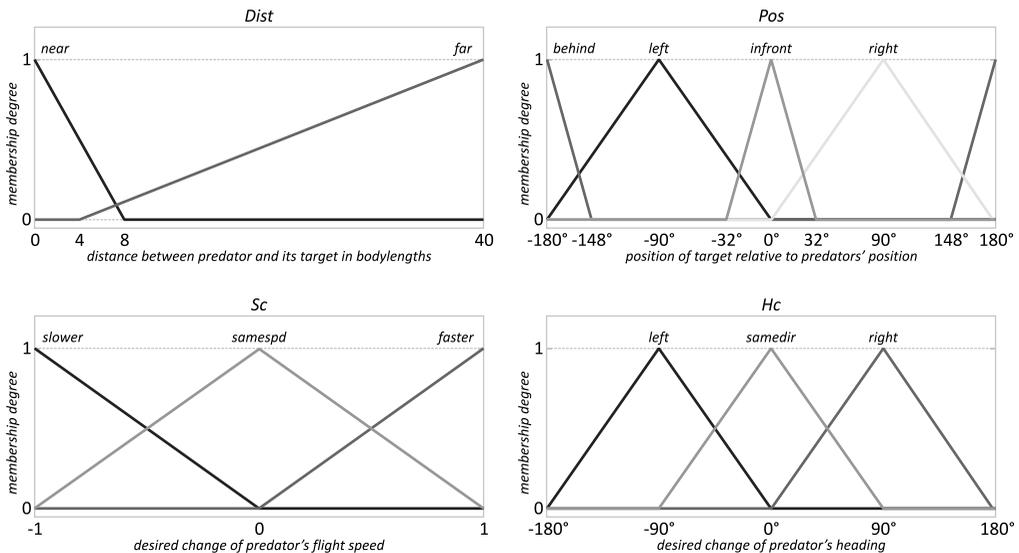
**Rules:**

```

if (Cs is too_fast) then (Sc is slower)
if (Cs is just_right) then (Sc is samespd)
if (Cs is too_slow) then (Sc is faster)
    
```

Figure 9. Detailed description of the regulate speed drive. On the membership function charts that describe speed, the value 1 represents the prey’s maximum speed, and -1 represents the negative of the prey’s maximum speed. While these are the desired changes in speed, the action selection stage ensures that the current speed of the observed individual never falls below the appropriate minimum speed (predator’s or prey’s).

The data extrapolated in the previous stage are fuzzified as singletons and used as inputs for the fuzzy rules. The fuzzy variables, membership functions, and control rules for the hide drive can be seen in Figure 8. Figure 9 presents the regulate-speed drive, and Figure 10 presents the seek drive. The fuzzy rules are evaluated per individual perceived animat and the fuzzy outputs aggregated.



**Rules:**

```

if (Pos is infront) then (Hc is samedir)
if (Pos is right) then (Hc is right)
if (Pos is left) then (Hc is left)
if (Pos is infront) then (Sc is faster)
if (Pos is left) and (Dist is near) then (Sc is slower)
if (Pos is right) and (Dist is near) then (Sc is slower)
    
```

Figure 10. Detailed description of the seek drive. On the membership function charts that describe speed, the value 1 represents the predator’s maximum speed, and -1 represents the negative of the predator’s maximum speed. While these are the desired changes in speed, the action selection stage ensures that the current speed of the observed individual never falls below the appropriate minimum speed (predator’s or prey’s).

The fuzzy outputs are then defuzzified and a force vector computed. This force vector represents the action that will fulfill the individual need. It gives the direction and magnitude of the individual drive (the desired change in speed and direction).

### A.3 Action Selection

In the action selection stage the force vectors resulting from individual drives are merged together and a resulting force vector computed. The merging is achieved through a simple weighted sum of

Table I. Default parameter values.

Parameter	Description	Default value
$\Delta t$	Time step	1 frame ( $\frac{1}{30}$ s)
$T$	Maximum length of one simulation	900 frames (30 s)
$v_{aM}$	Maximum speed of the predator animat	22 m/s
$v_{am}$	Minimum speed of the predator animat	8.8 m/s
$v_{pM}$	Maximum speed of prey animats	18 m/s
$v_{pm}$	Minimum speed of prey animats	7.2 m/s
$\varphi$	Animat field of view	300°
$n$	Number of influential nearest neighbors	7
$w_c$	Weight for cohesion drive	5
$w_s$	Weight for separation drive	5
$w_a$	Weight for alignment drive	3
$w_e$	Weight for hide drive	4
$w_{rs}$	Weight for regulate-speed drive	1
$w_h$	Weight for seek drive	1
$l$	Body length	0.2 m
	Fuzzification	Singleton
	Fuzzy conjunction	Product
	Fuzzy disjunction	Probabilistic sum
	Fuzzy implication	Product
	Fuzzy aggregation	Probabilistic sum
	Defuzzification	Center of gravity

the individual force vectors. The resulting force vector is interpreted as a Newtonian force, based on which the observed animat's speed, heading, and position are updated.

#### **A.4 Parameter Values**

All of our model's parameters were either extrapolated from relevant theoretical literature (speed, field of view, etc.) or tuned (fuzzy membership functions, action selection mixing weights, etc.) so that the resemblance of the displayed behavior to that observed in nature was visually as close as possible. For example, the action selection mixing weights have been configured so that the simulations visually resemble (as closely as possible) field observations of flocking behavior. In the prey's case these were 5, 5, 3, 4, and 1 for cohesion, separation, alignment, hide, and regulate speed, respectively. Table 1 presents all of the remaining parameters of the model.

