


Article

An Alignment-Free Explanation for Collective Predator Evasion in Moving Animal Groups

Daniel Strömbom *  and Catherine Futterman

Department of Biology, Lafayette College, Easton, PA 18042, USA

* Correspondence: stroembp@lafayette.edu

Abstract: Moving animal groups consist of many distinct individuals but can operate and function as one unit when performing different tasks. Effectively evading unexpected predator attacks is one primary task for many moving groups. The current explanation for predator evasion responses in moving animal groups require the individuals in the groups to interact via (velocity) alignment. However, experiments have shown that some animals do not use alignment. This suggests that another explanation for the predator evasion capacity in at least these species is needed. Here we establish that effective collective predator evasion does not require alignment, it can be induced via attraction and repulsion alone. We also show that speed differences between individuals that have directly observed the predator and those that have not influence evasion success and the speed of the collective evasion process, but are not required to induce the phenomenon. Our work here adds collective predator evasion to a number of phenomena previously thought to require alignment interactions that have recently been shown to emerge from attraction and repulsion alone. Based on our findings we suggest experiments and make predictions that may lead to a deeper understanding of not only collective predator evasion but also collective motion in general.

Keywords: collective behavior; collective motion; evasion dynamics; escape wave; self-propelled particle model; alignment-free; flocking; disruptive dynamics; complex system



Citation: Strömbom, D.; Futterman, C. An Alignment-Free Explanation for Collective Predator Evasion in Moving Animal Groups. *Dynamics* **2023**, *3*, 793–802. <https://doi.org/10.3390/dynamics3040043>

Academic Editor: Christos Volos

Received: 10 October 2023

Revised: 11 November 2023

Accepted: 11 November 2023

Published: 15 November 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Despite being made up of many distinct individuals, moving animal groups often appear to operate as one unit [1,2]. They are self-organizing aggregates that can assume a variety of group shapes, change group shape, and collectively perform a number of tasks [3–6] such as collective decision making [7], migration [8,9], foraging [10], and predator evasion [11]. Accomplishing these tasks requires that local information can spread effectively in the group. In particular, information about a predator attack at a specific location in the group must propagate through the group and result in a collective evasive response [12]. Empirical studies in animals across taxa, including birds and fish, have investigated the effect of predator attacks on moving groups and characterized the group response to these attacks. In particular, several studies have shown that the response is mediated through the initiation and spread of escape waves through the group in birds [11,13], fish [14–16], and insects [17]. Herbert-Read et al. 2015 [16] conducted experiments where schools of pacific blue-eyes (*Pseudomugil signifer*) moved in an annulus-shaped shallow water tank, and when the school approached a particular region in the tank, a piston shot out to simulate a predator attack. When undisturbed, the school assumed a polarized group configuration and swam around the annulus. When the piston shot out, in most trials, a small proportion of fish closest to it turned and swam directly away from simulated predator at an increased speed. These few fast evading fish then influenced other fish to also turn until the whole school had switched direction and continued to move away from the predator.

The standard explanation for how moving groups form and function is that each individual interacts locally with its nearby neighbors via some combination of three social

forces, attraction, repulsion, and (velocity) alignment [5]. Theoretical studies using so-called self-propelled particle (spp) models have shown that a combination of these three forces at the individual level is sufficient to produce a range of stable groups [18–26], as well as groups that can perform collective decision making [27], migration, foraging, and predator evasion. In particular, various aspects of collective predator evasion have been studied using models that include alignment interactions [11,16,28–32]. However, empirical studies have established that several species of fish appear to not rely on alignment to organize their schools [33,34]; so an alternative explanation for this phenomenon in, at least, these species is required.

Recently, a number of studies have shown that several properties of moving animal groups previously thought to require the alignment interaction can be generated without it [35–43]. For example, attraction alone and combinations of attraction and repulsion have been shown sufficient to generate all three standard group types that alignment-based models can generate, including polarized (or aligned) groups [36,41,44] previously thought to require alignment interactions. Alignment-free models have also been shown capable of generating more disruptive phenomena, e.g., groups that spontaneously transition from one group type to another [42,43], as exemplified by schools of golden shiner fish [45]. Such dynamics had not previously been reported as producible using spp models and had even been conjectured impossible to generate using models of this type due to their inherent averaging of interactions [34].

Given the capacity of these recent alignment-free models to generate disruptive phenomena, investigating whether they can provide an attraction-and-repulsion-based explanation for collective predator evasion behavior in moving animal groups should be explored. This investigation is particularly important because several animals are thought to rely on attraction and repulsion alone to organize their groups [33,34,42,43]. This approach could also yield experimentally testable predictions for predator evasion in animals known to use alignment-free interactions. Additionally, comparing characteristics of alignment-free and alignment-based predator evasion may provide a deeper understanding of this phenomenon across taxa.

2. Model and Methods

Here, we adapt the self-propelled particle model introduced in [44] and subsequently shown capable of generating disruptive phenomena in [42,43]. In summary, in this model N particles are moving around at constant speed δ . Each particle interacts with other particles within a distance of R from it, excluding those in a blind zone defined by an angle β behind the particle relative to its direction of travel. The particles that a particle is interacting with are referred to as its neighbors. On each timestep t , each particle determines its neighbors and updates its heading based on attractive and repulsive interactions with its current neighbors. See [42,43] for a full description of this base model. Here, we adapt this model to mimic the setup in the Herbert-Read et al. 2015 experiments [16]. The modifications and changes to the original model are described below.

1. The space on which the particles are moving is restricted to an annular region, modeled as two concentric circles with particles confined to move between them. We use the same slip boundary conditions as in [42,43], modified to work with these circular boundaries;
2. The particles are initialized in a polarized configuration (as observed in experiments) moving clockwise (CW) in the annular region. See Figure 1a;
3. As the group of particles approach a specified point with coordinates (x_p, y_p) located inside the annular region ahead of the moving group, a predator attack is simulated at a specified time t_p . All particles that are within a distance of R_p from the predator attack point (x_p, y_p) detect the predator when it becomes active at time t_p and are strongly repelled directly away from it. See Figure 1b,c. More specifically, if a particle i is within R_p of the predator point, its heading update has an additional predator

evasion term \bar{R}^p added to Equation (1) in [43]. The most general form of the heading update formula used here is

$$\bar{D}_{i,t+1} = b\hat{D}_{i,t} + c\hat{C}_{i,t} + a\hat{A}_{i,t} + r\bar{F}_{i,t} + r_p\bar{R}_{i,t}^p + e\hat{e}_{i,t}, \tag{1}$$

where $\hat{D}_{i,t}$ is particle i 's current heading, $\hat{C}_{i,t}$ is the normalized direction towards the local center of mass of its neighbors except those in the blind zone, $\hat{A}_{i,t}$ is the normalized average heading of its neighbors, $\bar{F}_{i,t}$ is a local distance dependent repulsion term, $\bar{R}_{i,t}^p$ is the repulsion directly away from the predator, $\hat{e}_{i,t}$ is a heading noise term, and the parameters a, b, c, e, r, r_p specify the relative strengths of the different interaction terms. For a detailed description of all terms except the predator repulsion term see [43,44]. The predator repulsion term $\bar{R}_{i,t}^p$ has exactly the same form as the local repulsion term $\bar{F}_{i,t}$, but is calculated using only the predator coordinate (x_p, y_p) instead of the coordinates of all neighbors of the particle;

4. To investigate the potential impacts of a difference in speeds between particles that have and those that have not detected the predator, we add a parameter δ_s in some analyses. We denote the ratio of the speed of particles that have detected the predator (δ_s) and the speed of those that have not (δ) by $\Delta = \delta_s/\delta$. So, if there is no difference in speed between those that have detected it and those that have not, then $\Delta = 1$, if those that have detected it moves twice as fast as those that have not, then $\Delta = 2$, and so on.

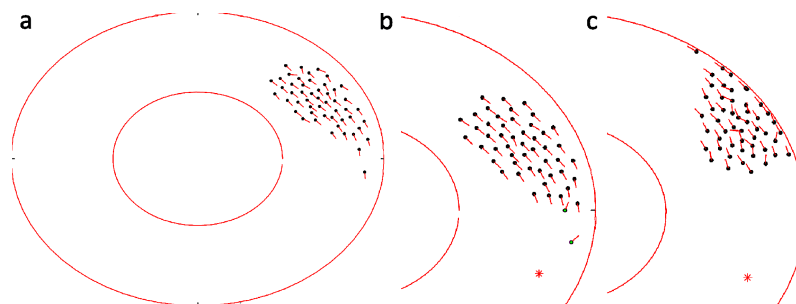


Figure 1. Simulation environment. (a) Screenshot of a simulation in the annular region with a group of particles moving clockwise. Black dots represent the particles and the red rods indicate each particle's direction of travel. The instantaneous alignment ϕ_t of this group at this time t will be positive and large in absolute value (between 0.75 and 1). (b) The simulated predator attack has commenced. The red asterisk (*) indicates the predator attack point and two particles at the front of the group (green dots) have detected the predator and are moving directly away from it. As particles continue to switch from the clockwise to the counterclockwise direction, the instantaneous alignment ϕ_t will decrease from its positive large value. (c) Following the predator attack, the entire group has switched direction and are all moving in the counterclockwise direction away from the predator. The instantaneous alignment ϕ_t of this group at this time t will be negative and large in absolute value (between -0.75 and -1).

2.1. Measures

To quantify the simulation results, we use two measures similar to those defined and used in [16]. The main difference in implementation is that we do not partition the arena into 36 segments for the calculations but instead exclusively use the actual particle positions throughout.

1. The arc distance between an individual particle i and the predator point (x_p, y_p) at time t , which we denote by $d_{i,t}$. $d_{i,t}$ is calculated as the length of circular arc between the angle of the predator point and the angle of particle i at time t , with radius equal to the Euclidean distance from fish i 's coordinates at time t $(x_{i,t}, y_{i,t})$ to the center of the annular region $(0,0)$;
2. The instantaneous alignment of the group at time t (ϕ_t) can be used to determine whether the group is moving clockwise (CW) or counterclockwise (CCW) in the

annular region. It is calculated by first calculating the relative orientation of each particle i at time t via $\chi_{i,t} = \sin^{-1}(\sin(\alpha - \beta))$, where α is the angle of the particle and β is the angle of the annular region radius going through the particle position at time t . $\chi_{i,t} = -\pi/2$ if the particle is moving CW and $\chi_{i,t} = \pi/2$ if it is moving CCW. The instantaneous alignment of the group at time t is then calculated as the average of the relative orientations of all the N particles at time t through

$$\phi_t = \frac{2}{\pi N} \sum_{i=1}^N \chi_{i,t}. \quad (2)$$

The instantaneous alignment ϕ_t ranges from -1 to 1 and provides information about whether the group is moving clockwise (CW) or counterclockwise (CCW). An ideal group moving clockwise at time t will have $\phi_t = 1$, and one moving counterclockwise will have $\phi_t = -1$. In practice though, because no group, of either real animals or simulated particles, will be moving in an ideal fashion, we classify a group at time t as moving clockwise if $\phi_t \in [0.75, 1]$ and counterclockwise if $\phi_t \in [-0.75, -1]$.

2.2. Simulations

Given that the analyses in [16] focused on 51 fish, here, we perform 1450 simulations for each of eight different cases for 51 particles: four with attraction and repulsion only ($a = 0$ in Equation (1)), and four with alignment added ($a = 0.5$ in Equation (1)). The four different cases for each correspond to different speed ratios $\Delta = 1, 2, 3,$ and 4 . At the start of each simulation, particle positions and headings are initialized to be in a polarized configuration moving clockwise. The base configuration for this was obtained by simulating the model from random initial conditions in the annular region without predator attacks until it adopted a polarized configuration moving clockwise. At the start of each simulation, this base configuration is then perturbed both with respect to particle positions and headings to obtain unique initial conditions for each of the $1450 \times 8 = 11,600$ simulations carried out. The predator attack point (x_p, y_p) was chosen to be at coordinates $(17, -7)$ because with this value a few particles at the front of the moving group tend to be within R_p of the predator point (x_p, y_p) at the predator attack time $t_p = 35$. These few particles will detect the predator and be assigned the higher speed δ_s corresponding to that particular case. The other parameters in the heading update (Equation (1)) were set to $c = 2, d = 0.5, r = 1.5, r_p = 5, \delta = 0.2$ and $e = 1/14$. The blind angle $\beta = 3.2$ was chosen based on the findings in [43]. At this value, a group tends to adopt a polarized configuration, but is close enough to the bistability region to reconfigure in response to perturbations. In each of the 11,600 simulations, we collect the trajectory of each particle over time. This trajectory information was then used to present representative simulations of the key cases we seek to compare, i.e., collective predator evasive behavior generated by attraction and repulsion alone without any speed difference ($\Delta = 1$) and with the largest speed difference used ($\Delta = 4$), and the same speed differences when alignment was added. Using the trajectories of all particle through each simulation, we calculated the distance between each particle and the predator attack point through time. The result is plotted in Figure 2. The predator attack time $t_p = 35$ and predator detection radius $R_p = 8$ are also superimposed on each plot. This trajectory information was also used to calculate the instantaneous alignment over time in each simulation for each case. The instantaneous alignment was then used to calculate the median over the 1450 simulations in each of the eight cases to generate the average evasion curves in Figure 3, as well as the mean, and 95% confidence intervals to generate supplementary Figures S1 and S2. Due to non-normal instantaneous alignment measurement distributions, all confidence intervals presented are bootstrap confidence intervals calculated using the Matlab function `bootci` with 2000 bootstrap samples. To investigate how evasion success depends on the interaction between the interaction rules and speed differences, we ran 7000 simulations for each Δ from 1 to 4 in increments of 0.1 for each of the interaction rules and measured the instantaneous alignment over time. This information was then used to calculate the mean proportion of simulations, as well

as 95% confidence intervals, in each of the 62 cases (2 interaction rules and 31 speed differences) that resulted in a successful group evasive maneuver away from the predator, using the criteria that if $\phi_t < -0.75$ at some time t after the predator attack time t_p , then the group turned away from the predator and is moving away from it counterclockwise. The results of these analyses were used to create Figure 4 and Table 1. See the Data Availability Statement for information about how to access the Matlab code used for these analyses.

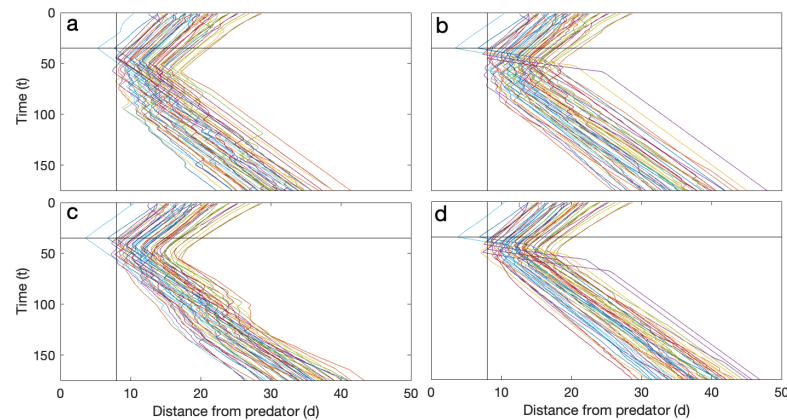


Figure 2. The collective evasion process. Each panel shows the angular distance of each particle to the predator point over time (colored lines). The horizontal line indicates the predator time $t_p = 35$ and the vertical line indicated the predator detection range $R_p = 8$. In each case, we see a similar process. The distance between each particle and the predator decreases up until the predator attack at $t = 35$, at which point the particles that are closer to the predator than $R_p = 8$ (left of the vertical line) start moving away from the predator and influence other particles (which have not detected the predator) to switch their directions also in a cascade-type fashion. The two top panels (a,b) show the process when only attraction and repulsion are operating with no speed difference $\Delta = 1$ (a) and with a large speed difference $\Delta = 4$ (b). The two bottom panels (c,d) show the process when alignment is operating, with no speed difference $\Delta = 1$ (c) and with a large speed difference $\Delta = 4$ (d). By comparing the panels on the same row, we can observe the effects of differing speeds, and by comparing the panels in the same column, we can see the effects of including alignment. While there are differences, in particular, in that higher speed differences result in smoother transitions and more stable group motion post evasion maneuver, the basic evasion behavior is the same.

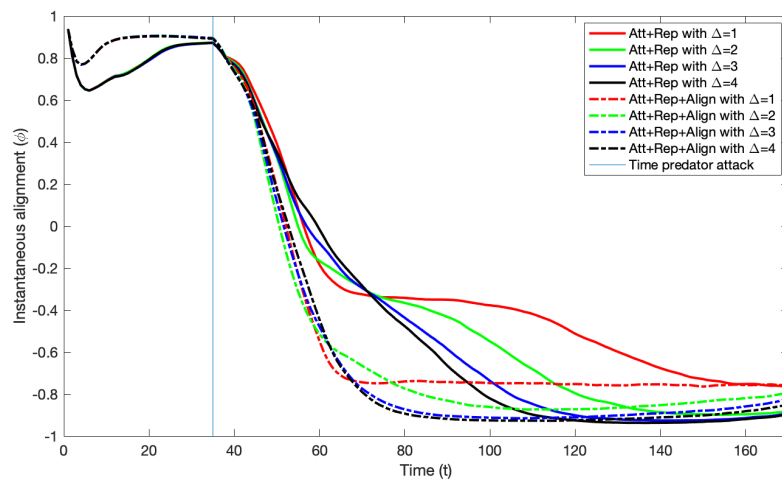


Figure 3. Comparison of the average instantaneous alignment (ϕ) over time for the eight different cases. Solid curves correspond to attraction and repulsion only, dashed lines correspond to alignment included. Curve color indicates the speed difference $\Delta = 1$ (red), $\Delta = 2$ (green), $\Delta = 3$ (blue), and $\Delta = 4$ (black). The horizontal line represents the predator attack time $t_p = 35$ and we note that at this

time, all curves drop rapidly from a high $\phi \approx 0.9$. Initially, all curves drop at comparable rates but as time progresses, the alignment curves drop quicker, especially when the ϕ drops below -0.2 , i.e., after the average heading of the group has turned away from the direction of the predator. We also note that these are averages and that the successful turn rate is significantly lower for the smaller speed differences than the higher (Table 1), which contributes to the flattening out of the green and red curves (due to failure to turn, splits, etc). See Video S1 for example simulations of each of the eight cases.

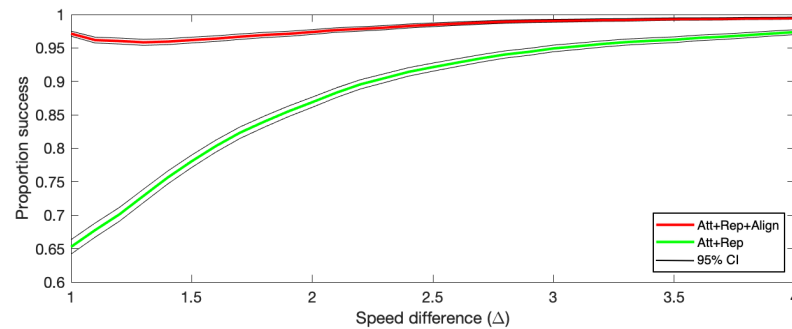


Figure 4. Evasion success as a function of speed difference. The green curve shows the mean evasion success proportion for the attraction-and-repulsion-only model, and the red curve the mean evasion success proportion for the attraction, repulsion, and alignment model. The black lines represent the 95% bootstrap confidence intervals.

Table 1. Probability of successful evasion depending on the interaction rule used and speed differences between particles that have detected the predator and those that have not. We note that increasing speed differences (Δ) increase evasion success for both interaction rules.

	$\Delta = 1$	$\Delta = 2$	$\Delta = 3$	$\Delta = 4$
Att + Rep	0.6527	0.8728	0.9483	0.9736
Att + Rep + Align	0.9713	0.9744	0.9907	0.9945

3. Results

Alignment interactions are not required to induce collective predator evasion in moving groups. Attraction and repulsion alone are sufficient. Figure 2a,b shows the distance d from the predator to each particle over time in the alignment-free model, and Figure 2c,d show the corresponding trajectories in the alignment-based model. In all cases, we note that all particles approach the predator location, the predator is activated at $t = 35$ and at this time, the few particles that are within a distance of $R_p = 8$ from the predator move directly away from it and influences the other particles, which have not detected the predator, to turn until the whole group has turned and collectively move away from the predator, and, while there are noticeable differences between the trajectories in the different panels, the basic dynamics are the same, implying that alignment is not strictly required to induce this phenomenon.

Speed differences between individuals that detect the predator and those that do not influence the success rate of and stabilize the predator evasion process, but are not strictly required for it to occur. Comparing Figure 2a with Figure 2b, and Figure 2c with Figure 2d, we note that the post attack trajectories smooth out faster when there is a large speed difference Δ . This implies that the evasion process is faster and the whole group switches to its new direction in a smoother fashion when speed differences are large.

Figure 3 shows the average evasion behavior over time for all the eight cases, and Video S1 shows example simulations of each. We note that, on average, there are noticeable differences between evasive behavior generated by alignment-free (solid lines) and alignment-based (dashed lines) models in Figure 3 in that, while they are relatively similar up until $\phi \approx -0.2$, i.e., when there is a net instantaneous alignment in the direction away from the predator but a significant part of the group has yet to turn, after that, the behavior

of two model types diverge. Alignment-based models exhibit a smooth switch, on average, whereas the alignment-free models exhibit a slower turn rate after $\phi \approx -0.2$. We also note that speed difference plays a significant role on the average behavior. In particular, the higher speed difference cases ($\Delta = 3$ and 4) for both model types exhibit smooth decreases to low ϕ values (< -0.75), indicating successful evasions, on average. The low-speed-difference curves ($\Delta = 1$ and 2) exhibit a different type of interrupted turning behavior, on average. This is a consequence of the fact that the lower speed difference cases have lower evasion success rates and are more susceptible to failing to turn and pass the predator or experience group splits. See supplementary materials for versions of Figure 3 with mean and 95% confidence interval information (Figure S1) and the raw instantaneous alignment measurements over all simulations (Figure S2). The proportion of successful evasions, including 95% confidence interval information, as a function of speed difference Δ for both interaction rules is presented in Figure 4. The green curve shows the proportion of success for attraction and repulsion only, and the red curve for attraction, repulsion, and alignment. The red curve shows that the alignment-based model has a success rate of above 0.95 for all speeds, and the green curve shows that the alignment-free model's evasion success increases from about 0.65 at no speed difference ($\Delta = 1$) to about 0.97 for $\Delta = 4$. Overall, in both cases, the success proportion increases with increasing speed difference. Table 1 shows the specific proportions for integer speed differences. We note that for large Δ values, the success proportions are high for both interaction rules, that alignment-based models have higher success rate overall, and that the alignment-free model with no speed difference has only a 64% success percentage, which explains the flattening of the red solid curve after -0.2 .

4. Discussion

Alignment interactions are not required to induce collective predator evasion in moving groups. This finding provides an explanation for collective predator evasion in moving animal groups for animals that do not use alignment interactions to organize their groups. This extends our mechanistic understanding of this phenomena beyond the alignment-based explanation provided by the models in [16,28–32].

Speed differences between individuals that detect the predator and those that do not influence the success rate of and stabilize the evasion process, but are not strictly required for it to occur (Figures 2–4). In [16], alignment and speed differences were isolated as primarily responsible for the model's predator evasion capacity via escape waves consistent with data. While our findings indicate that predator evasion and escape-wave-like behavior does not strictly depend on either of these, we do find that both alignment and speed differences improve the rate and smoothness of the response (Figure 2 and 3). This suggests that despite not being technically required, they may be highly relevant to predator evasion in some real moving animal groups; in particular, because some fish have been shown to use alignment, e.g., barred flagtails *Kuhlia mugil* [46], and speed changes during attacks are well documented across taxa [11,13,14,17,47,48].

Our work makes a number of predictions that could be experimentally tested by re-running the experiments performed in [16] with fish that are known to use alignment, and fish that are known to not use alignment. Suitable candidates for lab experiments with fish that do not use alignment are golden shiners *Notemigonus crysoleucas* [34] and mosquitofish *Gambusia holbrooki* [33], while barred flagtails *Kuhlia mugil* are a suitable candidate for fish that use alignment [46]. The results presented in Figure 3 predict that fish that rely on alignment and those that do not will exhibit similar responses early in the process after the attack, but that fish that do not use alignment will be slower in completing the latter part of the process compared to fish that rely on alignment. For fish using alignment, we predict that there will be no noticeable slowing of the process midway. Furthermore, measuring the speed difference between fish that detect the predator and those that do not also yields predictions of the relative success rate of evasions once it is known whether alignment is used or not (Figure 4 and Table 1).

In addition, the observed escape wave speed differences in three key studies of the phenomena in fish [14–16] may perhaps be partially explained by the different species using different interaction rules. In particular, whether the species use alignment or not, and what the speed difference between the primary predator detectors and non-detectors is. The average escape wave speeds found in the three studies were 0.29 m/s [16], 4.1–10.3 m/s [15], and 11.8–15.1 m/s [14]. We are unable to find any information about which interaction rules the three species used in these studies are thought to use, in particular, if either of them have been shown to rely on alignment. While there may be other explanations for this discrepancy in speed, such as size differences in the fish used as pointed out in [16], the rules employed by the different species may also influence this. If hypothetically, no other factor is responsible, based on our results, we would guess that the pacific blue-eyes used in [16] rely on attraction and repulsion only, and the fish in [14,15] both rely on alignment. Testing whether pacific blue-eyes rely on alignment or not should be straightforward, given that the trajectory data exists, and the methods used to determine whether alignment is operating in golden shiners, mosquitofish, and barred flagtails should be available from [33,34,46].

Performing these kinds of experiments for a range of species might also be useful in the other direction, i.e., to infer interaction rules. It is known that inferring interaction rules from data of groups in a steady state is less informative than inferences based on data from the approach to the stable state [49]. Immediately following the predator attacks in [14,16], the group is out of the steady state and recovering towards one over time. This phase could provide particularly useful data for inferring, or at least distinguishing between proposed, interaction rules by the approach described in paragraph 3 of the discussion in [41].

Here, we have shown that collective predator evasion is yet another phenomenon previously thought to require alignment interactions that does not. In addition to the discovery that polarized (or aligned) groups can be generated from attraction alone in combination with a range of biologically plausible auxiliary locomotion-related assumptions [41], including asynchrony [36,39], anticipation [40], and burst-and-glide dynamics [41], combinations of attraction and repulsion alone have also been shown to have the capacity to generate polarized (or aligned) groups in a range of fundamentally different types of models [23,35,37,38]. It is also noteworthy that the above-mentioned models not only can produce polarized (or aligned) groups without including an alignment interaction but almost all of them have also been shown capable of generating the other two standard groups of collective motion, i.e., mills/tori and disorganized swarms. This indicates that alignment is not required to explain general features of stable collective motion in moving animal groups. However, until recently, it was unclear (and actually conjectured impossible on theoretical grounds [34]), whether any spp model, alignment-based or otherwise, could generate disruptive phenomena such as bistability and transitioning between groups types. Interestingly, it was recently established that both alignment-free and alignment-based models can actually generate these types of disruptive behaviors [42,43]. Through the current work, we can now add collective predator evasion to the list of phenomena that are explainable by attraction and repulsion alone without the requirement of alignment. Through these findings, over the past decade, it is becoming increasingly plausible that the observed group level alignment and other phenomena in many real moving animal groups emerges from an interplay of attraction and repulsion alone, rather than from an explicit alignment interaction. This challenges the current dogma of collective motion, which states that “Attraction is a prerequisite for the formation of social aggregations, repulsion restricts crowding and prevents collisions and alignment is proposed to produce coordinated motion.” [5].

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/dynamics3040043/s1>. Figure S1: Mean and 95% bootstrap confidence intervals of the instantaneous alignment ϕ over the 1450 simulation for each of the eight cases. The black thin curves around each colored curve represents the 95% confidence intervals. We note that in all cases they are very narrow, sometimes so narrow that they are difficult to distinguish from the colored curves; Figure S2: Measured instantaneous alignment in each simulation. Each panel shows the measured instantaneous alignment over time in each of the 1450 simulations for that case, with the median superimposed as a thicker line; Video S1: Example simulations for each of the eight cases.

Author Contributions: Conceptualization, D.S.; Data curation, D.S.; Formal analysis, D.S. and C.F.; Investigation, D.S. and C.F.; Methodology, D.S. and C.F.; Software, D.S.; Visualization, D.S.; Writing—original draft, D.S.; Writing—review and editing, D.S. and C.F. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: The data and Matlab code needed to regenerate all figures and tables in this manuscript and run new simulations can be found at <https://github.com/danielstrombom/Evasion> (accessed on 10 November 2023).

Conflicts of Interest: The authors declare no conflict of interest.

Abbreviation

The following abbreviation is used in this manuscript:

spp self-propelled particle

References

1. Camazine, S.; Deneubourg, J.L.; Franks, N.R.; Sneyd, J.; Theraula, G.; Bonabeau, E. *Self-Organization in Biological Systems*; Princeton University Press: Princeton, NJ, USA, 2001.
2. Sumpter, D.J.T. *Collective Animal B*; Princeton University Press: Princeton, NJ, USA, 2010.
3. Shaw, E. Schooling fishes: The school, a truly egalitarian form of organization in which all members of the group are alike in influence, offers substantial benefits to its participants. *Am. Sci.* **1978**, *66*, 166–175.
4. Heppner, F.H. Avian flight formations. *Bird-Banding* **1974**, *45*, 160–169. [[CrossRef](#)]
5. Ward, A.; Webster, M. *Sociality: The Behaviour of Group-Living Animals*; Springer: Berlin/Heidelberg, Germany, 2016.
6. Herbert-Read, J.E. Understanding how animal groups achieve coordinated movement. *J. Exp. Biol.* **2016**, *219*, 2971–2983. [[CrossRef](#)]
7. Ward, A.J.; Herbert-Read, J.E.; Sumpter, D.J.; Krause, J. Fast and accurate decisions through collective vigilance in fish shoals. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 2312–2315. [[CrossRef](#)]
8. Flack, A.; Nagy, M.; Fiedler, W.; Couzin, I.D.; Wikelski, M. From local collective behavior to global migratory patterns in white storks. *Science* **2018**, *360*, 911–914. [[CrossRef](#)]
9. Couzin, I.D. Collective animal migration. *Curr. Biol.* **2018**, *28*, R976–R980. [[CrossRef](#)]
10. Evans, J.C.; Torney, C.J.; Votier, S.C.; Dall, S.R. Social information use and collective foraging in a pursuit diving seabird. *PLoS ONE* **2019**, *14*, e0222600. [[CrossRef](#)]
11. Procaccini, A.; Orlandi, A.; Cavagna, A.; Giardina, I.; Zoratto, F.; Santucci, D.; Chiarotti, F.; Hemelrijk, C.K.; Alleva, E.; Parisi, G.; et al. Propagating waves in starling, *Sturnus vulgaris*, flocks under predation. *Anim. Behav.* **2011**, *82*, 759–765. [[CrossRef](#)]
12. Sumpter, D.; Buhl, J.; Biro, D.; Couzin, I. Information transfer in moving animal groups. *Theory Biosci.* **2008**, *127*, 177–186. [[CrossRef](#)]
13. Beauchamp, G. Flock size and density influence speed of escape waves in semipalmated sandpipers. *Anim. Behav.* **2012**, *83*, 1125–1129. [[CrossRef](#)]
14. Radakov, D.V. *Schooling in the Ecology of Fish*; John Wiley & Sons: Hoboken, NJ, USA, 1973.
15. Marras, S.; Batty, R.S.; Domenici, P. Information transfer and antipredator maneuvers in schooling herring. *Adapt. Behav.* **2012**, *20*, 44–56. [[CrossRef](#)]
16. Herbert-Read, J.E.; Buhl, J.; Hu, F.; Ward, A.J.; Sumpter, D.J. Initiation and spread of escape waves within animal groups. *R. Soc. Open Sci.* **2015**, *2*, 140355. [[CrossRef](#)]
17. Treherne, J.E.; Foster, W.A. Group transmission of predator avoidance behaviour in a marine insect: the Trafalgar effect. *Anim. Behav.* **1981**, *29*, 911–917. [[CrossRef](#)]
18. Aoki, I. A simulation study on the schooling mechanism in fish. *Bull. Jpn. Soc. Fish.* **1982**, *48*, 1081–1088. [[CrossRef](#)]
19. Huth, A.; Wissel, C. The simulation of the movement of fish schools. *J. Theor. Biol.* **1992**, *156*, 365–385. [[CrossRef](#)]

20. Couzin, I.D.; Krause, J.; James, R.; Ruxton, G.D.; Franks, N.R. Collective memory and spatial sorting in animal groups. *J. Theor. Biol.* **2002**, *218*, 1–11. [[CrossRef](#)] [[PubMed](#)]
21. Vicsek, T.; Zafeiris, A. Collective motion. *Phys. Rep.* **2012**, *517*, 71–140. [[CrossRef](#)]
22. Reynolds, C.W. Flocks, herds and schools: A distributed behavioral model. *Siggraph Comput. Graph* **1987**, *21*, 25–34. [[CrossRef](#)]
23. D’Orsogna, M.R.; Chuang, Y.L.; Bertozzi, A.L.; Chayes, L.S. Self-propelled particles with soft-core interactions: patterns, stability, and collapse. *Phys. Rev. Lett.* **2006**, *96*, 104302. [[CrossRef](#)]
24. Romenskyy, M.; Herbert-Read, J.E.; Ward, A.J.; Sumpter, D.J. Body size affects the strength of social interactions and spatial organization of a schooling fish (*Pseudomugil signifer*). *Open Sci.* **2017**, *4*, 161056. [[CrossRef](#)]
25. Cambui, D.S. Collective behavior states in animal groups. *Mod. Phys. Lett. B* **2017**, *31*, 1750054. [[CrossRef](#)]
26. Newman, J.P.; Sayama, H. Effect of sensory blind zones on milling behavior in a dynamic self-propelled particle model. *Phys. Rev. E* **2008**, *78*, 011913. [[CrossRef](#)] [[PubMed](#)]
27. Couzin, I.D.; Krause, J.; Franks, N.R.; Levin, S.A. Effective leadership and decision-making in animal groups on the move. *Nature* **2005**, *433*, 513–516. [[CrossRef](#)] [[PubMed](#)]
28. Papadopoulou, M.; Hildenbrandt, H.; Sankey, D.W.; Portugal, S.J.; Hemelrijk, C.K. Emergence of splits and collective turns in pigeon flocks under predation. *R. Soc. Open Sci.* **2022**, *9*, 211898. [[CrossRef](#)]
29. Papadopoulou, M.; Hildenbrandt, H.; Sankey, D.W.; Portugal, S.J.; Hemelrijk, C.K. Self-organization of collective escape in pigeon flocks. *PLoS Comput. Biol.* **2022**, *18*, e1009772. [[CrossRef](#)]
30. Hemelrijk, C.K.; van Zuidam, L.; Hildenbrandt, H. What underlies waves of agitation in starling flocks. *Behav. Ecol. Sociobiol.* **2015**, *69*, 755–764. [[CrossRef](#)] [[PubMed](#)]
31. Hildenbrandt, H.; Carere, C.; Hemelrijk, C.K. Self-organized aerial displays of thousands of starlings: a model. *Behav. Ecol.* **2010**, *21*, 1349–1359. [[CrossRef](#)]
32. Inada, Y.; Kawachi, K. Order and flexibility in the motion of fish schools. *J. Theor. Biol.* **2002**, *214*, 371–387. [[CrossRef](#)]
33. Herbert-Read, J.E.; Perna, A.; Mann, R.P.; Schaerf, T.M.; Sumpter, D.J.; Ward, A.J. Inferring the rules of interaction of shoaling fish. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 18726–18731. [[CrossRef](#)]
34. Katz, Y.; Tunström, K.; Ioannou, C.C.; Huepe, C.; Couzin, I.D. Inferring the structure and dynamics of interactions in schooling fish. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 18720–18725. [[CrossRef](#)]
35. Romanczuk, P.; Couzin, I.D.; Schimansky-Geier, L. Collective motion due to individual escape and pursuit response. *Phys. Rev. Lett.* **2009**, *102*, 010602. [[CrossRef](#)] [[PubMed](#)]
36. Strömbom, D. Collective motion from local attraction. *J. Theor. Biol.* **2011**, *283*, 145–151. [[CrossRef](#)] [[PubMed](#)]
37. Ferrante, E.; Turgut, A.E.; Dorigo, M.; Huepe, C. Elasticity-based mechanism for the collective motion of self-propelled particles with springlike interactions: A model system for natural and artificial swarms. *Phys. Rev. Lett.* **2013**, *111*, 268302. [[CrossRef](#)] [[PubMed](#)]
38. Barberis, L.; Peruani, F. Large-scale patterns in a minimal cognitive flocking model: incidental leaders, nematic patterns, and aggregates. *Phys. Rev. Lett.* **2016**, *117*, 248001. [[CrossRef](#)]
39. Strömbom, D.; Hassan, T.; Hunter Greis, W.; Antia, A. Asynchrony induces polarization in attraction-based models of collective motion. *R. Soc. Open Sci.* **2019**, *6*, 190381. [[CrossRef](#)]
40. Strömbom, D.; Antia, A. Anticipation induces polarized collective motion in attraction based models. *Northeast. J. Complex Syst. (NEJCS)* **2021**, *3*, 2. [[CrossRef](#)]
41. Strömbom, D.; Tulevech, G. Attraction vs. alignment as drivers of collective motion. *Front. Appl. Math. Stat.* **2022**, *7*, 717523. [[CrossRef](#)]
42. Strömbom, D.; Nickerson, S.; Fatterman, C.; DiFazio, A.; Costello, C.; Tunström, K. Bistability and switching behavior in moving animal groups. *Northeast. J. Complex Syst. (NEJCS)* **2022**, *4*, 1. [[CrossRef](#)]
43. Strömbom, D.; Tulevech, G.; Giunta, R.; Cullen, Z. Asymmetric Interactions Induce Bistability and Switching Behavior in Models of Collective Motion. *Dynamics* **2022**, *2*, 462–472. [[CrossRef](#)]
44. Strömbom, D.; Siljestam, M.; Park, J.; Sumpter, D.J. The shape and dynamics of local attraction. *Eur. Phys. J. Spec. Top.* **2015**, *224*, 3311–3323. [[CrossRef](#)]
45. Tunström, K.; Katz, Y.; Ioannou, C.C.; Huepe, C.; Lutz, M.J.; Couzin, I.D. Collective states, multistability and transitional behavior in schooling fish. *PLoS Comput. Biol.* **2013**, *9*, e1002915. [[CrossRef](#)] [[PubMed](#)]
46. Gautrais, J.; Ginelli, F.; Fournier, R.; Blanco, S.; Soria, M.; Chaté, H.; Theraulaz, G. Deciphering interactions in moving animal groups. *PLoS Comput. Biol.* **2012**, *8*, e1002678. [[CrossRef](#)] [[PubMed](#)]
47. Michaelsen, T.C.; Byrkjedal, I. ‘Magic carpet’ flight in shorebirds attacked by raptors on a migrational stopover site. *Ardea* **2002**, *90*, 167–171.
48. O’Brien, D. Description of escape responses of krill (Crustacea: Euphausiacea), with particular reference to swarming behavior and the size and proximity of the predator. *J. Crustac. Biol.* **1987**, *7*, 449–457. [[CrossRef](#)]
49. Mann, R.P. Bayesian inference for identifying interaction rules in moving animal groups. *PLoS ONE* **2011**, *6*, e22827. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.