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Report

The Dynamics of Coordinated Group Hunting and Collective Information Transfer among Schooling Prey

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Summary

Predator-prey interactions are vital to the stability of many ecosystems [1]. Yet, few studies have considered how they are mediated due to substantial challenges in quantifying behavior over appropriate temporal and spatial scales. Here, we employ high-resolution sonar imaging to track the motion and interactions among predatory fish and their schooling prey in a natural environment. In particular, we address the relationship between predator attack behavior and the capacity for prey to respond both directly and through collective propagation of changes in velocity by group members [2–6]. To do so, we investigated a large number of attacks and estimated per capita risk during attack and its relation to the size, shape, and internal structure of prey groups. Predators were found to frequently form coordinated hunting groups, with up to five individuals attacking in line formation. Attacks were associated with increased fragmentation and irregularities in the spatial structure of prey groups, features that inhibit collective information transfer among prey. Prey group fragmentation, likely facilitated by predator line formation, increased (estimated) per capita risk of prey, provided prey schools were maintained below a threshold size of approximately 2 m^2. Our results highlight the importance of collective behavior to the strategies employed by both predators and prey under conditions of considerable informational constraints.

Results and Discussion

Collective Response to Predator Attack

A principal challenge to determining the functional characteristics of collective animal behavior has been to quantify it under natural contexts in natural environments. Antipredator benefits of grouping are widely believed to be one of the main drivers of the evolution of aggregation in many species [7]. Although properties such as the confusion effect [8], dilution of risk [9], predator detection [10], and risk abatement [11] have been investigated in multiple theoretical and experimental studies [7], dynamical properties of predator-prey interactions have received much less attention. In recent years, however, there has been growing realization that distributed transfer of velocity information, facilitated by social interactions, may contribute substantially to the robust yet highly responsive nature of many animal groups [5, 6, 12]. Measuring such properties in animal groups remains a key challenge.

We investigated the dynamic interactions between a piscivorous predator (spotted sea trout, *Cynoscion nebulosus*) and the response behavior of its schooling prey (juvenile Gulf menhaden, *Brevoortia patronus*) (see Table S1 available online), a highly abundant and ecologically important species in the estuarine and near-shore ecosystems along the coast of the Gulf of Mexico [13]. Menhaden use these estuarine habitats as nursery areas and form large fission-fusion populations. In order to quantify the motion of both predator and prey interactions, we employed high-frequency imaging sonar (DIDSON, Sound Metrics, Lake Forest Park, WA) that has unprecedented spatial (~2 cm) and temporal (8 Hz) resolution (so-called "acoustic video") within a two-dimensional fan spanning an area of 24 m^2 (Figure S1). This allowed us to relate the fast-timescale local interactions between predators and prey to larger-scale collective behaviors.

A large number of predator-prey interactions were observed during our 2 hr sampling period; the number of predators simultaneously interacting with the schools within our field of view varied between 0 and 17 throughout the period, with an average of 2.7 individuals. Gulf menhaden schools are characteristically highly dynamic and reactive when responding to predators (see Movie S1).

Typical attacks by predatory sea trout involve approaching prey from behind (Figure 1) with an estimated average speed of 0.249 ± 0.002 m/s (SEM). The mean prey speed, estimated by optical flow (see Supplemental Experimental Procedures), in the half space in front of the predator (Figure 2) was 0.195 ± 0.008 m/s and decreased to a mean flow speed over the sonar field of view of 0.117 ± 0.001 m/s. Prey fish move more slowly than the predators, but due to their size they are more maneuverable [14].

The typical response of the prey fish to the presence of predators was determined by calculating the mean density and direction of prey around the predator (Figure 2; see Figure S2 for the mean velocity). The density indicates that prey are rarely found within a 20 cm range of the predator. The response direction reveals that prey ahead of the predator tend to escape by moving directly away, a form of "flash expansion" [15]. Once the predator has passed, fish turn to face the passing predator, a behavioral pattern previously described as a "fountain effect" [15, 16]. It appears from Figure 2 that the range of social influence among prey fish may extend beyond immediate neighbors despite the high turbidity of this environment [17], a property that may impact the capacity for predators to hunt effectively.

In recent years, the long-range transfer of behavioral change, such as direction, speed, or density, has been quantified in a number of animal groups, including swarming

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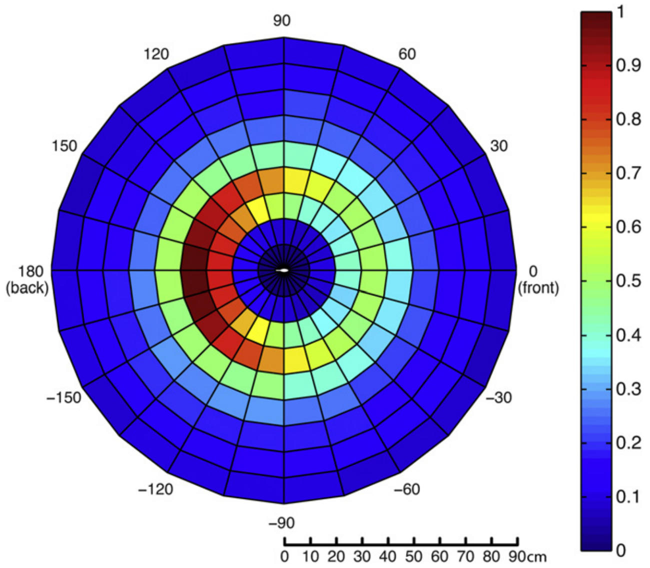

Figure 1. The Distribution of the Nearest Predator around a Representative Focal Prey

The prey is located in the center of the plot facing right (to scale). Each bin represents a 10 cm by 15° area. The color map represents the scaled number of predator detections in each bin, where 1 is equal to the maximum number of prey within a bin divided by the bin area. The predator tends to attack the prey from behind. See Figure S1 for the data processing techniques and Movie S1 for visualization.

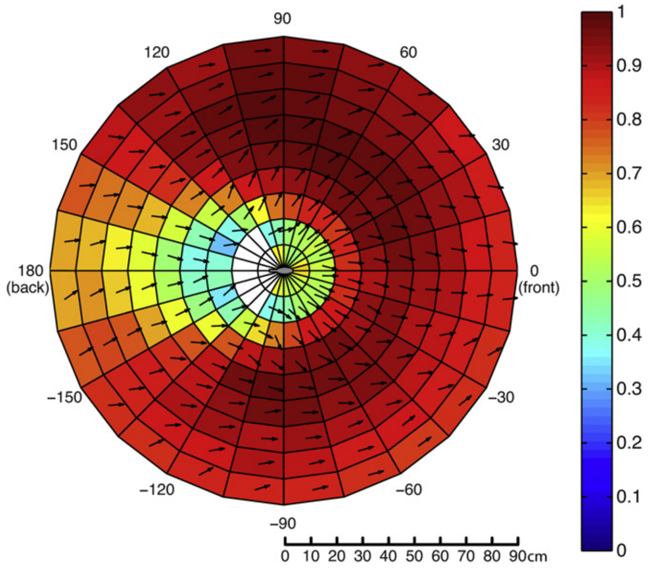

Figure 2. The Distribution and Average Direction of Prey around Predators

The predator is located in the center of the plot facing right (to scale). The arrows show the average direction of all prey surrounding the predator. Each bin represents a 10 cm by 15° area. The color map shows the scaled number of prey detections in each bin, where 1 is equal to the maximum number of predators within a bin divided by the bin area. Note that the prey are rarely closer than 20 cm to the predator. Some predators can be detected as prey, and to ensure no interference, the data points (pixels) behind the predators were removed. See Figure S2 for examples of false detections.

locusts [5], flocking birds [12], and vast oceanic herring schools [18]. For example, Makris et al. [18] demonstrate how compressional density waves can propagate over tens of kilometers in herring schools at a speed that is an order of magnitude greater than the typical individual swim speed. Similar phenomena have been observed in bird flocks including dunlin (*Calidris alpina*) [19] and the European starling (*Sternus vulgaris*) [20], suggesting that this type of behavior may be generic to highly coordinated groups. A notable property of groups is that collective response can effectively span a system regardless of its size, so-called "scale-free" behavior. In starlings, for example, local (topologically mediated) interactions among the birds [6] result in measurable correlated domains of orientation and speed that span the entire group [12]. Thus, flocks can effectively behave as a singular unit, despite individual interactions being limited to a fixed number of neighbors.

The biological implications of these long-range correlations are currently unknown, but it has been suggested [12, 21, 22] that collective information transfer is important, if not essential, to survival in many group-living species. However, these collective properties have not been quantified in relation to response to external perturbations in the field, such as attack by predators. In order to measure the range over which prey fish can socially transmit velocity information, we calculated the correlation length ξ of velocity fluctuations, as described by Cavagna et al. [12]. To do so, for each school, we subtracted the direction of travel from the prey velocity flow field and calculated the correlation metrics based on the velocity, direction, and speed (see Supplemental Experimental Procedures for details). As with European starling flocks [12], we found that the correlation length increases linearly with the square root of the school area (velocity correlation shown in Figure 3; direction and speed correlations shown in Figure S3). This provides support for the hypothesis that social interactions provide strong and long-range coherence across the group [23]. Note that the square root of the area is only a proxy for group size, because schools can be irregular in shape (see below) and some schools are only partially ensonified, i.e., part of the group may be outside the detection field of the sonar. Nevertheless, the correlation length shows a clear scaling with the linear size proxy of the group, suggesting that this is a robust feature.

Prey School Size and Individual Risk

Numerous studies have shown that encounter rate saturates with prey group size, resulting in reduced per capita risk in larger groups [9, 11, 24]. Despite the relatively high spatial and temporal resolution of our sonar, it is not yet possible to directly measure capture efficiency by predators. However, if we make the assumption that risk of capture increases when prey are in close proximity (<30 cm) to the predator, we can determine a rational proxy for per capita risk experienced by prey in different school sizes (Figure 4A). The 30 cm threshold was chosen to span the typical nearest distance between predators and prey ($\sim$20 cm; see Figure 1) and is twice the length of the predators (Table S1). We demonstrate that our results are robust to changes of this threshold distance below.

Risk proxy is greater for smaller group sizes (generalized linear model [GLM]: $F_{1,5755} = 759.21$, $p < 0.01$; Table S2; Figure 4A) and increases steeply for groups below $\sim 2\ m^2$. Thus, for larger groups there is an approximately linear relationship between encounter rate and group size (Figure S4), likely due to the low visibility and high turbidity of our system (15 nephelometric turbidity units). Experiments to simulate visual

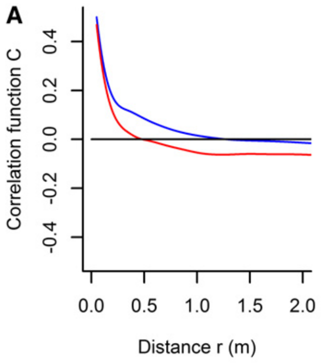

Figure 3. Behavioral Correlations across the Schools

(A) The red and blue lines are the velocity correlation function C(r) for the square root of the school areas of 1.75 m and 3.5 m, respectively, as a function of distance r. The zero crossing defines the correlation length ξ.
(B) The mean velocity correlation length ± SEM as a function of the square root of school area. The red and blue circles correspond to the red and blue curve in (A), respectively.
See Figure S3 for correlation lengths based on velocity, speed, and direction.

reaction determined reaction distances to be 20 cm in conditions similar to ours [17] for prey fish. Although we were not able to test the visual response of predators, it is highly likely that the full spatial extent of prey groups is not visible to them. In low-visibility situations, like ours, sensory modalities like the lateral line are likely to be important for intra- and interspecific interactions [25]. However, although prey wake trails can in principle be detected by the lateral line, this requires the predator to follow directly in the trail of prey [26]. It is unclear whether this type of strategy is relevant to a situation such as this where prey move in a dynamic and complex way. However, regardless of the sensory modalities involved, informational constraints are likely to result in effects of density that are dependent on spatial scale, i.e., the result of the interaction between predator and prey changes with the scale over which density is measured (see also [24] and [8]).

Predator Coordinated Attack and Influence on Prey Schools

That there may be effectively no limit to the range over which velocity information can propagate within prey schools (see Figure 3) suggests that individuals in larger groups are responsive to predators over a greater range. If true, this could impact the effectiveness of predators when hunting individuals in large groups because those prey will be able to transfer directional information over a distance much greater than that at which the predators can influence ("control") prey behavior. This brings forth the question of how predators influence prey schools.

We found that predatory sea trout exhibit highly coordinated behavior when hunting. The position of the nearest predator, from a focal predator's point of view, demonstrates clear group structure: the individuals form lines in which neighbors are spaced four to five body lengths ahead of and/or behind each other (Figure 4B). Predators spend about one-quarter of their time in such coordinated groups, mostly in pairs, but groups of up to five predators were detected in our study. As can be seen from the vacuole (area devoid of prey) extending between 50 and 100 cm behind a predator (Figure 2), it appears that predator grouping may function to maintain incoherence in the prey school, effectively impeding prey from closing the vacuole behind a given predator.

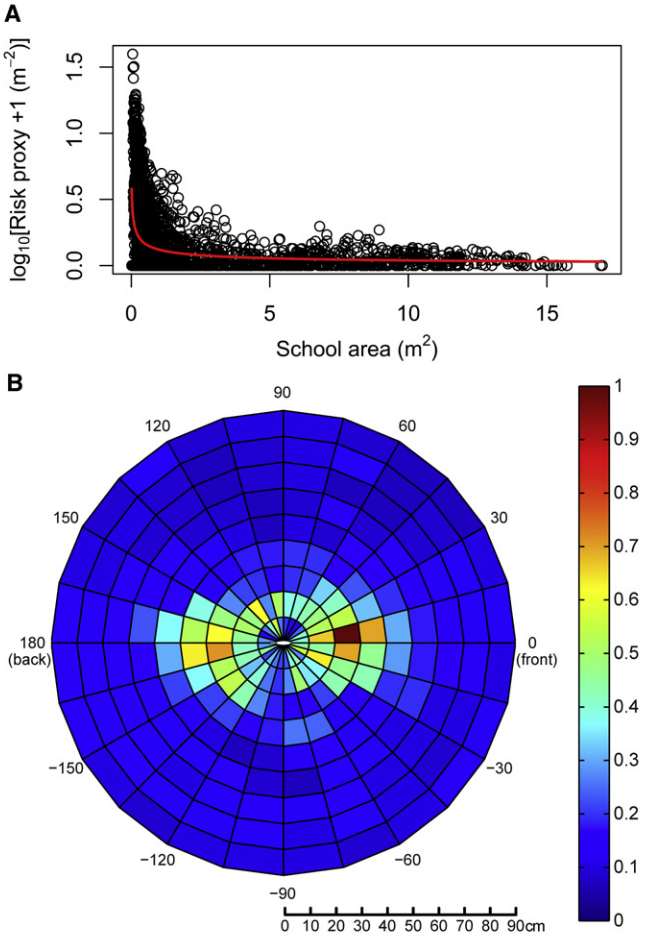

Figure 4. How Predation Affects Risk and Prey School Properties

(A) Risk proxy as a function of school area. Circles are individual data points, and the red line is the model fit (see Table S2 for model details).
(B) Predators tend to attack in a line formation, suggesting coordination. The focal predator is located in the center of the figure facing right (to scale). The color map shows the scaled number of predators detected in each bin. Each bin represents a 10 cm by 15° area.
See Figure S4 for how predation affects other prey school properties.

From inspecting the image sequences (Movie S1), vacuoles behind the predators are clearly visible, and more irregular prey school boundaries are observed as a consequence of the attacks. We also observed that parts of the attacked school often split, and that these fragments may subsequently rejoin the original school. Qualitatively, it seems that predators induce irregularities within, and split, prey schools. It is therefore plausible, following our analysis of collective information transfer in groups (see above), that predator attacks could inhibit collective antipredator responses and increase per capita risk (Figure S4). To test this, we investigated the role of attacks on school size, school shape, and velocity correlation length (Table S3).

From the prey's perspective, there are more proximate predators per group member when they are in smaller schools (Figure 4A). Consistent with predators acting to break up groups as indicated by our sonar image sequences (Movie S1), prey schools close to a predator are significantly smaller than those experienced by a randomly placed predator (Figure S4; difference = 1.4 m^2, t test, $t = -11.7$, df = 575, $p < 0.001$). This bias toward smaller schools could be caused by the predators actively targeting such groups, although this is unlikely given the short visual range in this system. Instead, attacks may act to repeatedly split schools. In support of this, smaller groups persisted for a significantly less time than larger schools (Spearman's rank: $\rho = 0.35$, $p < 0.01$), suggesting that smaller groups are in a transient state caused by the perturbation of attacks before the fish rejoin into larger schools. Predation is also associated with increased irregularity in the shape of schools (i.e., greater perimeter relative to area; GLM: $F_{1,5754} = 154.57$, $p < 0.001$), which is likely to be an intermediate step in fragmenting schools.

Fragmentation induced by attacks reduces correlation length by decreasing group size (Figure 3). In addition, a greater number of predators is associated with reduced correlation lengths, while controlling for group size and shape (GLM: group size: likelihood ratio test $[LRT]_{1,5753} = 20{,}468.8$, $p < 0.001$; number of predators: $LRT_{1,5753} = 33.3$, $p = 0.001$; the effect of shoal shape was only marginally significant: $LRT_{1,5753} = 3.8$, $p = 0.05136$). To ensure that our results were not sensitive to the 30 cm threshold distance used to associate predators to groups, we performed our analysis for a range of different distances. These results are presented in Table S2 and demonstrate that our results are robust to this measure. Although we acknowledge that we cannot fully control for pseudoreplication in such a field study, due to the possibility of repeated detection of the same school over time, autocorrelation between schools is not a confounding factor (see Supplemental Experimental Procedures). Furthermore, the highly dynamic fission-fusion nature of this population is likely to result in substantial mixing of individuals, as found in other fish populations [26].

Conclusions

Interactions between predators and prey have been a focus of modern ecology due to their substantial contribution to population, community, and ecosystem properties [1, 27]. We investigated interactions among piscivorous spotted sea trout and Gulf menhaden. We show the predator-prey relationship between these species to depend on relatively local and fast-timescale predator-prey interactions (often on the order of seconds or less), and yet investigations at this scale are rare due to the inherent difficulty in quantification. Our approach allowed us to relate important functional properties such as information transfer among prey, how predators coordinate attacks, and how predators influence the dynamic fission-fusion properties of prey schools in their natural environment.

Observed correlation lengths in larger schools were well in excess of the typical interindividual distance between prey fish, and also that between predators and prey (see Figures 1 and 2). This provides evidence that prey can use relevant velocity information from conspecifics before they are even able to directly detect a threat. In contrast to previous tests of this effect [2, 4], the low visibility of our system (~20 cm) allows us to rule out any possible direct reaction of distant prey to the approaching predator (or predators). Studies have shown that predator preference is often stronger for larger (or more conspicuous) groups [24, 28, 29]. This can even result in a higher per capita attack rate for larger groups in some species [28]. However, in these cases [28, 29] the success rate was found to be lower for larger group sizes, more than compensating for the increased attack risk. In the present study, we found that per capita risk does decrease as group size increases, but that this relationship is strong only for relatively small groups. Although other mechanisms may promote coordination among hunting predators, the consequence is that the predators break up schools, as well as decreasing spatial coherence within schools, likely limiting the collective response of prey fish and increasing capture rate. Although it is not possible to infer causation from our data, it is plausible that this group hunting strategy has evolved specifically to disrupt the collective information transfer properties that prey in groups possess.

Our study highlights the importance of collective information transfer and fast-timescale kinematics in predator-prey interactions. The methodology presented here demonstrates that high-frequency sonar can be used to make nonintrusive and quantitative observations of the motion and interactions of predators and prey in natural aquatic environments, could readily be modified to facilitate real-time observation for arbitrarily long periods of time, and hence could be used to quantify dynamics over extensive temporal scales. It would be useful to investigate whether predator-prey interactions remain stable over multiyear timescales, for example, and to relate the observed local predator-prey dynamics to ecosystem state variables, such as predator and prey densities, turbidity, and even anthropogenic influences [30].

Supplemental Information

Supplemental Information includes four figures, three tables, Supplemental Experimental Procedures, and one movie and can be found with this article online at doi:10.1016/j.cub.2012.04.050.

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