

## Three-dimensional predator–prey interactions: a computer simulation of bird flocks and aircraft

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Three-dimensional interactions between grouped aerial predators (frontal discs of aircraft engines), either linearly arrayed or clustered, and flocks of small birds were studied using interactive computer simulation techniques. Each predator modelled was orders of magnitude larger than an individual prey, but the prey flock was larger than each predator. Expected numbers of individual prey captured from flocks were determined for various predator speeds and trajectories, flock–predator initial distances and angles, and flock sizes, shapes, densities, trajectories, and speeds. Generally, larger predators and clustered predators caught more prey. The simulation techniques employed in this study may also prove useful in studies of predator–prey interactions between schools or swarms of small aquatic prey species and their much larger vertebrate predators, such as mysticete cetaceans. The study also provides a method to study problems associated with turbine aircraft engine damage caused by the ingestion of small flocking birds, as well as net sampling of organisms in open aquatic environments.

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Des techniques de simulation interactive à l'ordinateur ont permis d'évaluer les interactions tri-dimensionnelles entre des prédateurs aériens (disques frontaux de moteurs d'avions), regroupés selon un arrangement linéaire ou rassemblés en masse, et des bancs de petits oiseaux. Chaque prédateur simulé était d'un ordre de grandeur supérieur à celui d'une proie individuelle, mais le banc de proies était de taille supérieure à celle de chacun des prédateurs. Le nombre théorique de proies individuelles capturées dans les bancs a été déterminé en fonction de la vitesse du prédateur, de sa trajectoire, de la distance et de l'angle banc–prédateur au départ, de la taille du banc, de sa forme, de la densité des proies dans le banc, de la trajectoire et de la vitesse du banc. En général, les prédateurs de grande taille et les prédateurs rassemblés attrapent plus de proies. Les techniques de simulation employées au cours de cette étude peuvent aussi s'avérer utiles dans les études d'interactions prédateurs–proies entre des bancs de petites espèces de proies aquatiques et les vertébrés beaucoup plus gros qui sont leurs prédateurs, tels les cétacés mysticètes. Cette étude fournit aussi une méthode pour étudier les problèmes associés aux dommages que subissent les moteurs d'avions à la suite d'aspirations de petits oiseaux qui volent en bandes de même que les problèmes associés à l'échantillonnage au filet dans les milieux aquatiques ouverts.

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### Introduction

Predator–prey interactions can be categorized by a set of descriptors, including (i) groupings: single predator – single prey, single predator – grouped prey, grouped predators – single prey, or grouped predators – grouped prey (depending upon the species involved, a particular predator–prey interaction might include transitions between any of these grouping states); (ii) relative size of predators compared with their prey: predators larger (by various orders of magnitude), predators and prey of approximately the same size (within an order of magnitude), or predators smaller; (iii) predator feeding type: “filter” (many prey captured simultaneously per attack, strike, or bout) or particulate (single prey captured per attack, strike, or bout); (iv) dimensionality: one-, two-, or three-dimensional interaction; and (v) general environmental context in which the interaction occurs: aerial, terrestrial, aquatic, or a combination.

Certain sets of these descriptors cannot be exemplified by naturally occurring predator–prey interactions. For example, aerial predators that capture multiple smaller prey simultaneously appear to be absent in natural ecosystems. There also appears to be a lack of aerial predators that hunt in coordinated

groups. Such examples only seem to occur in aquatic environments, and many of these predators (e.g., mysticete cetaceans, certain teleostean and elasmobranch species) are many orders of magnitude larger than their prey. Human-manufactured “predators” (towed or pushed fish and plankton nets) have been introduced into aquatic environments to capture invertebrate and vertebrate prey. Many of these nets are not unlike natural predators in design and use, although their operation is more static in terms of pursuit behavior. Unlike the use of nets in aquatic systems, however, the use of turbine engines to power aircraft has resulted in the introduction into aerial environments of a “predator” without natural precedent. The introduction of such a novel predator into a system allows one to investigate simultaneously a number of questions about predator–prey interactions, including the following: how adaptive are flocking behavior and other prey antipredator responses when a larger, faster predator is introduced, and how successful are such predators at capturing prey?

To address these questions this study used computer simulation techniques to study interactions of aerial predators, modelled after the frontal area of turbine aircraft engines, and small flocking prey, modelled after the dunlin or red-backed sandpiper (*Calidris alpina*), a small migratory shorebird. In addition qualitative field observations were made of the

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behavior of dunlin and starling (*Sturnus vulgaris*) flocks in the presence of aircraft, and under attack by raptors.

## Methods

A moving three-dimensional Poisson model was chosen to describe the interactions between predators (sets of engine frontal areas) and prey (dunlin flocks). This model, incorporated into an interactive computer program, calculated the expected number of captures ( $E(\text{NC})$ ) of birds by each predator for each operator-supplied set of predator-prey trajectories and speeds. The model was also used to calculate, for individual predators, the exponential distribution of the interbird capture interval, its expected value, and its variance.

### The model

A flock of birds at a particular instant may be described probabilistically by associating a theoretical distribution with each spatial region  $R$ . This is the distribution of the random number ( $N(R)$ ) of birds within  $R$ . Consider a region  $S$  consisting of the union of several nonoverlapping regions  $R_1, R_2, \dots, R_n$ , and assume that a collection of these associated distributions will always satisfy the condition,  $N(S) = N(R_1) + N(R_2) + \dots + N(R_n)$ . The spatial Poisson process attributes a Poisson distribution to  $N(R)$  for each region  $R$ , and always renders independent the variables  $N(R_1), N(R_2), \dots, N(R_n)$ . A particular spatial Poisson process can then be completely specified by the expectation  $E(N(R))$  for each  $R$ . This can be done so that the following always is true:  $E(N(S)) = E(N(R_1)) + E(N(R_2)) + \dots + E(N(R_n))$ . A model for predator-flock collisions is obtained by specifying the region  $B$  occupied by a flock at time zero, located horizontally from the predator(s) along a specific trajectory. The simplest Poisson model specifies  $E(N(RB))$  to be proportional to the volume of the common overlap ( $RB$ ) of  $R$  and  $B$ . From this assumption the expected value  $E(\text{NC})$  of the random number of collisions ( $\text{NC}$ ) can be determined from the region of overlap of  $R$  and  $B$  and the total flock volume ( $\text{VT}$ ) and the volume of the flock swept out by a predator ( $\text{VS}$ ). The total number of birds in the flock is operator supplied. The total flock volume and volume swept out are calculated from other operator-supplied parameters (see below).

In practice, one writes a program enabling  $B$  to be any of a number of regions, each region centered at the origin (0,0,0), by employing a "standard"  $B$ , such as a sphere of radius  $l$  or a square with unit-length edges. In the present model solid spheres or ellipsoids are used. Dimensions ( $l$  = length,  $w$  = width,  $h$  = height) of the principal axes are supplied, and the orientation of the flock is determined by a supplied trajectory. The total volume of the flock is thus  $4\pi lwh/24$ , leaving the calculation of the volume swept out of the flock by the predator(s) ( $\text{VS}$ ) as the main computational problem. Each predator's prey-catching area (engine disc) is smaller than the total flock dimensions used here (although orders of magnitude larger than any individual flock member) and is treated as being aligned perpendicular to its own trajectory. Thus, the problem of calculating the swept-out volume,  $\text{VS} = \pi r^2 L$  (where  $r$  is the disc radius and  $L$  is the length of the line traced through the flock by the disc centre), reduces to the problem of calculating  $L$ .

The first phase of the operator-program interaction is the determination of an approximate collision configuration; the operator then can experiment with minor changes of that configuration. This is done by supplying a velocity vector ( $a = (a_x, a_y, a_z)'$ ) and the bird flock speed ( $|f|$ ). The operator supplies velocity in navigational coordinates, which are converted to the corresponding Cartesian vector. The operator also supplies the initial position vector ( $d$ ) as a reference point on predator 1, with respect to the flock;  $d = (-\delta_1, 0, 0)'$  is most convenient for this, meaning that the reference point starts out at an operator-supplied distance ( $\delta_1$ ) from the flock centre. To determine a Cartesian coordinate flock velocity vector ( $f$ ) which will result in a collision (given velocity and speed  $|f|$ ), one must find a collision time ( $t$ , in seconds) for which  $d + ta = tf$ , where  $dt + ta$  is the position in space of predator 1 and  $tf$  is the position of the flock centre at time  $t$ . One can verify that a solution exists precisely when for some  $t > 0$ ,  $(a_x - \delta_1/t)^2 + a_y^2 = |f|^2$ . If there is no such  $t$ , the program responds with "no collision

is possible; supply a higher flock speed or a different predator velocity or initial distance." If the test passes, the program responds with the smaller collision time ( $t$ ) and with the collision-producing flock velocity vector  $f = (1/t)d + a$ , communicating this to the operator in terms of navigational coordinates. The operator can then produce additional collisions by supplying values of  $a$ ,  $f$ , and  $d$  close to these initial ones.

The dimensions of the flock must be supplied next. At any time  $t > 0$ , the flock occupies the solid sphere or ellipsoid consisting of all points  $(xe_1 + ye_2 + ze_3 + tf)$  for which  $x^2 \leq l^2$ ,  $y^2 \leq w^2$ , and  $z^2 \leq h^2$ , where  $e_1 = f/|f|$  is the unit-length vector pointing in the direction of  $f$ , and  $e_2$  and  $e_3$  are perpendicular to  $e_1$  and to one another, and also of unit length. Writing  $d_i = (d_{ix}, d_{iy}, d_{iz})'$  for the initial centre point of the disc of predator  $i$ ,  $E$  for the matrix whose columns are the vectors  $e_1, e_2, e_3$ , and then  $x(t)$ ,  $y(t)$ , and  $z(t)$  for the coordinates of the vector  $E^{-1}(d_i + t(a - f))$ , one can verify that the disc of predator  $i$  is immersed in the bird flock precisely during the time interval when  $x(t)^2 \leq l^2$ ,  $y(t)^2 \leq w^2$ , and  $z(t)^2 \leq h^2$ . This interval is the common overlap, if any, of the interval between the two solutions of the quadratic equation  $x(t)^2 = l^2$ , with the interval between solutions of  $y(t)^2 = w^2$ , and with that of  $z(t)^2 = h^2$ . If no common overlap exists, no collisions occur.

Having thus calculated the duration  $t_i$  of immersion of each disc number  $i$  in the flock, the length of its path through the flock is  $L = |a-f|t_i$ .

The initial predator disc positions  $d_1, d_2, \dots, d_n$ , etc., are operator supplied as noted above. Vectors  $c_1 = (c_{1x}, c_{1y}, c_{1z})'$ ;  $c_2, \dots, c_n$ , etc., describe other predators' disc centre positions relative to predator disc 1.  $c_{ix}$  is the fore-aft position, on a line parallel with a longitudinal axis through the midline between all discs;  $c_{iy}$  is the left to right position; and  $c_{iz}$  is the top to bottom position, i.e., perpendicular to the longitudinal and horizontal axes. The properly oriented and located disc centre position vectors relative to the origin are the columns  $d_i$  of the matrix  $D = BC + (d, d, \dots)$ , where each column  $d$  is the aforementioned reference point displacement vector  $d$  and the columns of  $B$  are calculated exactly the way  $E$  was formed from  $f$ .

Finally, it is an attribute of the Poisson process that the random waiting time, from any instant during predator immersion in the flock until the next bird capture by that predator, has an exponential distribution. In the present context one can verify that its expected value is  $1/\lambda$ , where  $\lambda = \pi r^2 |a-f| E(\text{NC})/(\text{VT})$ , and where  $r$  is the predator disc radius,  $|a-f|$  is the relative predator-prey speed, and  $E(\text{NC})/(\text{VT})$  is the proportionality constant for our spatial Poisson process. A calculated value of  $1/\lambda$  should be compared with the time duration of immersion for that predator.

### Predator characteristics

Two predator groupings were simulated, representing two types of turbine-powered aircraft in common use: (i) four linearly aligned engine discs (DC-8), and (ii) three clustered or triangularly arranged discs (Boeing 727). Both linear and triangular disc arrays and their characteristics are presented in Fig. 1 as they would appear on the aircraft. However, in the simulations presented here only the disembodied frontal discs are treated. Predators (and their interactions with flocks) are described in a three-dimensional reference coordinate system, where the  $x$ -axis is along the predator's flight path, through the centre of the disc representing predator 1 (positive values ahead, negative values behind), axis  $y$  is perpendicular to  $x$  in the horizontal plane (positive values to the right (facing toward the direction of travel), negative values to the left), and axis  $z$  is perpendicular to the  $x$ - $y$  plane. At the start of each simulation the location of the centre of disc 1 (and thus the origin of the coordinate system) was established 5 m below the centre of the flock ( $z = 0$ ). Dynamic behaviors (changes in speed and direction during an interaction, i.e., actual pursuit of evading prey) are not incorporated into the simulations. Also, the entire area of each disc is assumed to enter and exit a flock at the same time; there is no angular separation between any part of the edge of a disc and a flock. The velocities (speed and trajectory) simulated for predators are those of aircraft during ascents and descents at airfields. These speeds are of the same order of magnitude as those of stooping peregrine falcons,

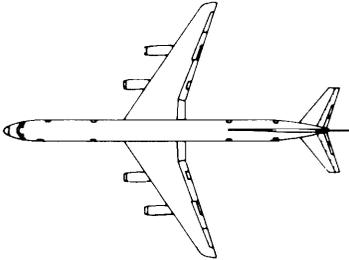
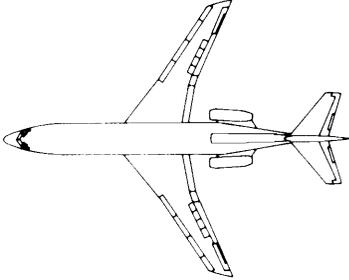
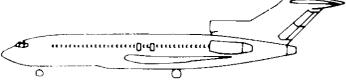
Type of Aircraft	DC-8			Boeing 727		
Top View						
Frontal View						
Side View						
Engine Centre Coordinates (m) & Engine Number	X	Y	Z	X	Y	Z
Starboard (1)	0	0	-5	0	0	-5
Starboard (2) Centre-727	3.38	-5.75	-5.45	0.04	-2.82	-2.62
Port (3)	3.38	-21.42	-5.45	0	-5.64	-5
Port (4)	0	-27.17	-5	-	-	-
Engine Area (m <sup>2</sup> )	1.049			0.7199		
Take-off Speed (m/s)	80			75		
Take-off Elevation (°)	13			13		
Take-off Bearing (°)	90			90		
Distance (m) from flock to Aircraft nose (mouth Engine 1)	76.72 (100)			76.72 (109.46)		

FIG. 1. Characteristics of predator frontal discs used in the simulated interactions with flocks of small birds. The frontal discs (engines) are figured as they would normally appear on aircraft; however, only the frontal discs were used in the simulations. Drawings not to scale.

*Falco peregrinus* (Meinertzhagen 1955), a natural predator of small flocking birds.

#### Flock characteristics

Flock characteristics used in the simulations are based upon observations of dunlin behaviour in response to aircraft and peregrine falcons at and near Vancouver International Airport, British Columbia, Canada. The base-line parameters for the simulated flocks included a sphere with a diameter of 10 m, density of 9.93 birds/m<sup>3</sup> (5200 birds in the flock), speed of 18.3793 m/s, and flight angle of elevation of 45°. The flock was initially positioned at a bearing 90° perpendicular to and, by convention, west of the centre of the disc representing predator 1, and 100 m (linear array) or 109.46 m (triangular array) directly in front

of this predator. The flock was assumed to have taken to the air just before the instant the predators began increasing their altitude (i.e., takeoff) with the result that for a 10 m diameter flock, the flock member at the lowest edge of the sphere or ellipsoid was at the same altitude as disc 1. These parameter values were chosen to ensure that a collision occurred, but the effect of varying each of the parameters independently was examined in the simulations. Prey speed and density figures used in the simulations are within the ranges reported by Major and Dill (1978) for dunlin and starling.

#### Field observations

Observations were made of dunlin and starling, species that form large flocks around Vancouver International Airport fields and shore-

line, and their natural predators, including peregrine falcons and marsh hawks (*Circus cyaneus*). The reactions of dunlin and starling to aircraft were also observed.

## Results

The results of the simulated three-dimensional predator–prey interactions are reported below and in Fig. 2. The expected number of captures was obtained as a function of flock bearing, angle of elevation, initial distance from predator 1, speed, lateral displacement (to the right or left of predator 1), height, shape, volume (cohesion), size, and density, and the speed and angle of elevation of the predator(s). The results for the four predators linearly aligned are summarized below first, followed by the results for three predators triangularly aligned, when such results differ substantially from the results for linear array simulations.

The precise values reported are less important than the general patterns revealed in the simulation data. Indeed, some results (e.g. the number of engines involved) are entirely dependent upon the initial conditions chosen.

### *Flock bearing (Fig. 2a)*

Two capture envelopes occurred for each of predators 1 and 2. Predator 1 captured prey between 79 and 101° (peak at 90° with a mean capture of 84 birds) and between 251 and 289° (peak at 270°, 101 birds). Predator 2 captured prey between 59 and 84° (peak at 73°, 82 birds) and between 274 and 316° (peak at 294°, 101 birds). The greatest total number of captures occurred where the two envelopes intersected: at 82° (114 birds) and 280° (158 birds). In the triangular array simulations predator 1 captured birds between 80 and 100° (peak at 90°, 63 birds) and between 253 and 287° (peak at 270°, 70 birds). Predator 2 captured birds between 78 and 88° (peak at 85°, 28 birds) and between 265 and 295° (peak at 280°, 62 birds). Predator 3 captured birds between 65 and 87° (peak at 75°, 63 birds) and between 273 and 308° (peak at 290°, 70 birds). The intersection of the capture envelopes for all three predators occurred at 85° (121 birds) and 280° (178 birds). For both linear and triangular array simulations the expected mean number of prey captured represented 2–3% of the 5200 prey in a flock.

### *Flock angle of elevation (Fig. 2b)*

Prey were only captured by predator 1 (because of the bearing chosen) and only for angles of elevation between 39 and 80° (positive values indicate birds moving in the same direction as (i.e., away from) the predators) and between –28 and –80° (i.e., towards on-rushing predators). The respective capture envelopes had peaks at 55° (102 birds) and –48° (103 birds). Captures by predator 1 in triangular array simulations occurred between 40 and 67° (peak at 50°, 70 birds) and between –29 and –67° (peak at –55°, 70 birds). Predator 2 captured birds between 50 and 76° (peak at 55°, 57 birds) and between –40 and –82° (peak at –55°, 58 birds). Intersection of the capture envelopes for predators 1 and 2 in the triangular array simulations occurred at 55° (123 birds) and –50° (124 birds). The number of prey captured represented approximately 1–2% of the flock.

### *Flock initial distance (Fig. 2c)*

Only predator 1 captured prey, at distances between 0 and 128 m (peak at 63 m, 103 birds). Approximately 2% of the flock was captured in these simulations. The shape of this curve is dependent upon the convention used here that the flock centre

ascends from a starting altitude 5 m above that at which the predators begin their ascent. If a difference in altitude had not been simulated, there would be no effect of initial distance, since both predator and prey vertical velocity vectors would have been invariant and equal. Thus, if other variables had led to captures at one initial distance, the same set of variables would have led to captures at other starting distances.

### *Flock speed (Fig. 2d)*

Predator 1 alone captured prey, between speeds of 16 and 26 m/s (peak at 21 m/s, 103 birds). All flock speeds examined were within the range of those recorded for dunlin and all resulted in captures. Only about 2% of each flock simulated was captured.

### *Flock lateral displacement (Fig. 2e)*

Predators 1 and 2 captured prey. Predator 1's prey capture envelope occurred at displacement distances (negative values to the right and positive values to the left of the centre of the disc representing predator 1) between –5 and +5 m (peak at 0 m, 84 birds). Predator 2 captured birds between distances of 0 and 10 m (peak at 6 m, 82 birds). The intersection of the capture envelopes for the two predators occurred at about 3 m (102 birds). All predators in the triangular array simulations captured prey. Predator 1's capture envelope occurred between displacements of –5 and +5 m (peak at 0 m, 63 birds). Predator 2 captured prey between 0 and 5 m (peak at 3 m, 29 birds). Predator 3 captured prey between 1 and 11 m (peak at 6 m, 63 birds). The intersection of the capture envelopes for the three predators occurred at a displacement of 3 m (127 birds). Approximately 0.5–3% of the prey were captured. Displacements beyond the envelopes presented in Fig. 2e likely have little meaning, particularly in a dynamic interaction in which the predator(s) could constantly modify their orientation towards an evading flock, keeping it close to the predator's centre line.

### *Flock height (Fig. 2f)*

Predator 1 alone captured prey, at heights between 2 and 14 m (peak at 8 m, 103 birds). Less than 3% of the prey were captured. The capture envelope is a result of the initial bearing angle of the flock from predator 1. As with lateral displacement, distances further from the envelope presented would have little meaning in dynamic interactions, where predators in pursuit could orient towards their prey.

### *Flock shape (Fig. 2g)*

In these simulations flock volume and number of individuals (thus density) were held constant. Only the length of the flock's major axis (concordant with the *x*-axis) was varied, between 10 and 100 m (a sphere and an ellipsoid, respectively). Only predator 1 captured prey at all flock lengths simulated. The greatest number of birds captured (94) occurred at a flock length of 20 m. In triangular array simulations only predator 1 captured birds, and the peak again occurred at 20 m (66 birds). The proportion of birds captured represented less than 2–3% of each flock.

### *Flock volume (Fig. 2h)*

In these simulations the number of birds was held constant (5200), while the spherical flock was increased in diameter, thus decreasing flock density. Predator 1 alone captured prey at all flock diameters simulated. The maximum number of prey (84 birds) was captured at the smallest dimension simulated (10 m, bird density of 9.93 birds/m<sup>3</sup>). The number of prey captured

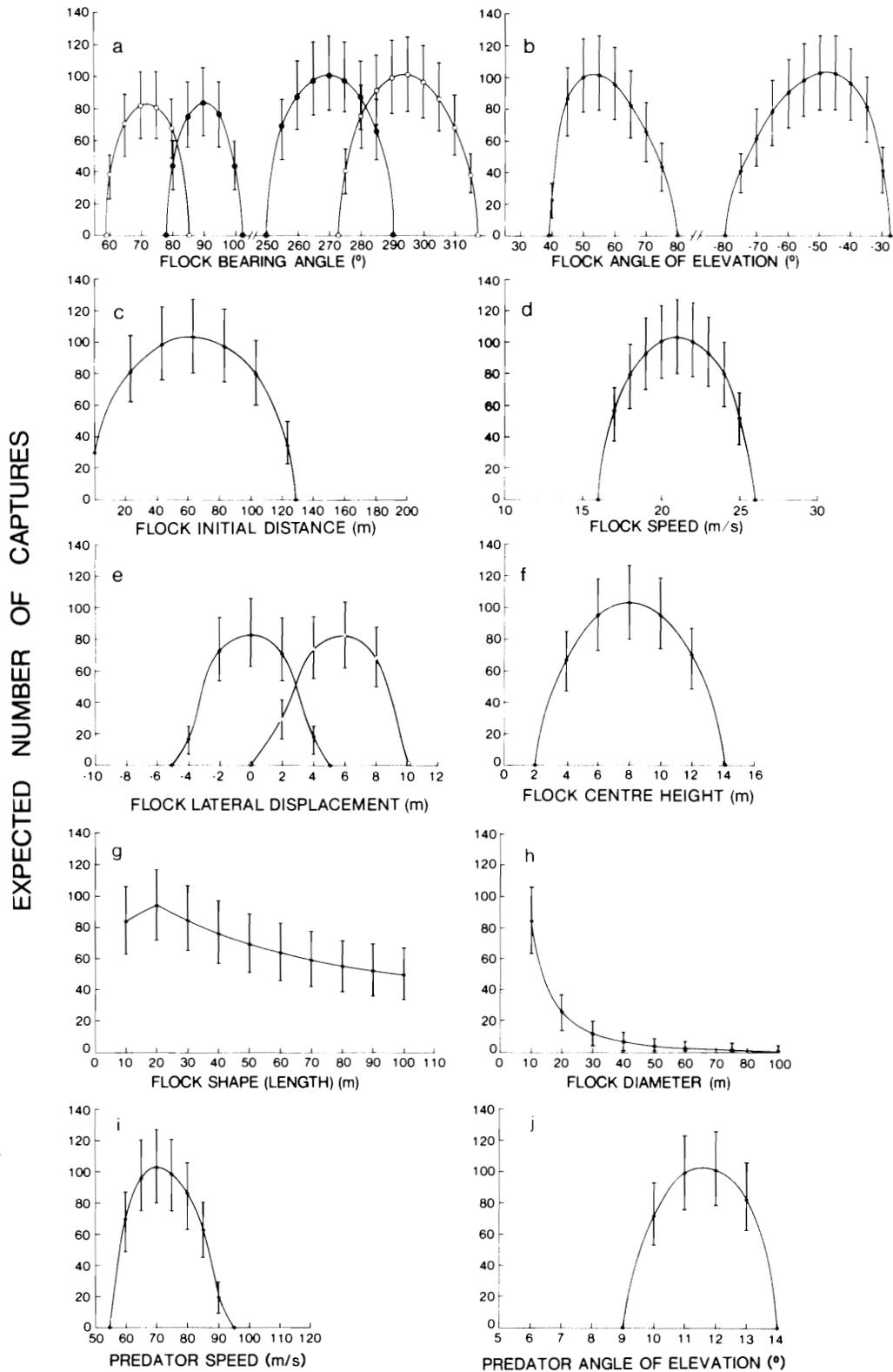


FIG. 2. Expected number of prey captured as a result of interactions between four linearly arrayed predators (characteristics as in Fig. 1; DC-8) and a flock of birds with the following initial characteristics: 10 m diameter sphere, 9.93 birds/m<sup>3</sup>, 5200 birds, speed 18.3793 m/s, angle of (flight) elevation 45°. Individual parameters were then varied as follows. (a) Flock bearing angle from predator. (b) Flock angle of (flight) elevation. (c) Flock centre's initial distance in front of predator 1. (d) Flock speed. (e) Lateral displacement of flock centre from predator 1's flight path. (f) Flock centre's height above predator 1. (g) Flock shape (length of major axis). (h) Flock volume or cohesion (diameter of sphere). (i) Predator speed. (j) Predator angle of (flight) elevation. Values presented are mean expected numbers of individual prey captured with 99% confidence intervals. Solid circles represent captures by predator 1; open circles, those by predator 2. Predators 3 and 4 did not capture prey in these simulations.

decreased as volume increased and density decreased. Results for the triangular predator array were similar.

#### *Flock size*

In these simulations sphere diameter (and volume) was increased, while the number of birds was covaried to maintain a density of 9.93 birds/m<sup>3</sup>. The number of birds captured by each predator increased linearly as the diameter of the flock increased. Predator 1 captured a minimum mean number of birds at a sphere diameter of 10 m; predator 2, at 15 m; predator 3, at about 45 m; and predator 4, at about 55 m. Results for the triangular predator array were similar.

#### *Flock density*

In these simulations sphere diameter (thus volume) was kept constant, while the number of birds (thus density) was increased. Only predator 1 captured prey. The number captured increased linearly with density; the minimum number of birds captured (0.2 birds) was from a flock of 10 birds (0.02 birds/m<sup>3</sup>), the smallest number simulated.

#### *Predator speed (Fig. 2i)*

Predator 1 captured prey at speeds between 55 and 95 m/s. The capture envelope had a peak at 70 m/s (103 birds). Predators 1 and 2 in the triangular array simulations captured prey: predator 1 captured prey at speeds between 55 and 85 m/s (peak at 70 m/s, 70 birds) and predator 2, at speeds between 55 and 75 m/s (peak at 65 m/s, 56 birds). The capture envelopes intersected at a speed of 65 m/s (125 birds captured). Faster moving predators passed above the flock and slower predators passed below in the simulations reported here. The number of prey captured represented less than 4% of each flock. As noted previously, the simulated predator speeds are similar to those of both man-made and natural predators.

#### *Predator angle of elevation (Fig. 2j)*

Prey were captured by predator 1 between angles of elevation of 9 and 14° (peak at 11.5°, 103 birds). Triangular array predators 1 and 2 captured birds, predator 1 between angles of 9 and 15° (peak at 12°, 71 birds) and predator 2 between angles of 9 and 13° (peak at 11°, 58 birds). The capture envelopes intersected at an angle of 12° (120 birds captured). Less than 3% of the prey were captured from flocks. Angles of elevation simulated were those normally employed by ascending and descending commercial aircraft at the speeds indicated. One can presume that natural predators would not be so limited in their approach angles.

#### *Interbird capture times*

The estimated rate at which birds were captured by predators was calculated only for the linear array grouping. For all values of flock bearing, angle of elevation, initial distance from predator 1, speed, lateral displacement from predator 1, height, and shape, and predator angle of elevation the rate of capture was approximately one capture every 0.0015 s. As the density of the flock increased (with constant flock volume), interbird capture times decreased from 0.05 s at a density of 0.019 birds/m<sup>3</sup> to 0.006 s at 1.91 birds/m<sup>3</sup> to 0.0006 s at 17.19 birds/m<sup>3</sup>. Similarly, as predator speed increased, birds were captured more rapidly (from one every 0.0022 s at 60 m/s to about one every 0.0008 s at 110 m/s. As the cohesion of the flock decreased (volume increased with a constant number of birds) interbird capture times also increased, as would be expected, from 0.0015 s at 10 m flock diameter, to 0.005 s at 15 m and 0.094 s at 40 m.

#### *Field observations*

Figures 3 and 4 each provide a series of photographs of typical reactions of a small flocking bird species, in these cases starlings, to approaching predators, man-made and natural. In Fig. 3 it appears that the approaching aircraft stimulates the birds to reduce flock length and interbird distances. However, because of the high relative speed and the trajectory of the aircraft past the flocking birds, the antipredator maneuver is not completed. Counts of individual birds were made in ten 1-cm squares from the projected and enlarged two-dimensional negatives: frame *a* ( $\bar{x}$  = 22.2 birds; range 10–30 birds), frame *c* ( $\bar{x}$  = 25.4; range 16–36). The counts indicate a slight, but nonsignificant increase in density.

The response of starlings to a marsh hawk (Fig. 4) is generally similar to their response to an aircraft. The starlings create an avoidance arc around the hawk and appear to increase their density immediately in front of it (frames *a* and *b*). Once the hawk turns away (frame *c*) the starling flock expands and the apparent density decreases (frames *d* and *e*).

Six interactions between peregrine falcons and starlings or dunlin were also observed. Single falcons stooped on flocks comprising birds numbering in the hundreds and thousands without success. The evasive maneuvers of each prey species, although generally similar, differed in detail. Both formed tight "balls" (spheres or ellipsoids) that constantly changed shape as the birds carried out highly erratic, protean maneuvers (Humphries and Driver 1967) including tight turning, wheeling, undulating, zig-zagging, reversing direction, and changing angles of elevation and bearing. Dunlin had a higher flight speed than starlings. When dunlin maneuvered to a position within a few degrees of the altitude of a falcon or were an estimated 50–100 m from it, fewer protean maneuvers were displayed; the birds simply increased their separation distance from the falcon by flying away in a straight line or with a slight zig-zag pattern. It appeared that dunlin had greater horizontal speed than did falcons and used their speed to outdistance the predator. Starlings appeared to rely more heavily on maneuvers and attempted to move above a falcon to evade it. In all attacks observed the falcon did not plunge into the flock, but passed close alongside it. In one instance an attacking falcon descended past, swung up under, rolled, and extended its talons upward towards a flock of dunlin. In all attacks it appeared that the falcon was attempting (unsuccessfully in these instances) to separate individuals from the flock, rather than to strike individuals within it.

The reactions of both starlings and dunlin to approaching aircraft were similar to their reactions to natural predators. In all observations the trajectory and speed of the aircraft took them past the flocks. Starling flocks usually attempted to maneuver by turning away perpendicular to the path of the aircraft. Dunlin, however, occasionally attempted to outdistance the approaching aircraft, flying down the length of the runway rather than off to the side. Captures were not observed, either because the dunlin eventually left the runway at a slight angle or because the aircraft changed direction, by taking off or (upon landing) by stopping or turning to taxi in another direction before reaching the birds.

#### **Discussion**

Three-dimensional interactions between relatively large predators and their prey, which are often orders of magnitude smaller but are captured en masse, have not as yet been the subject of systematic study. The simulations presented here of

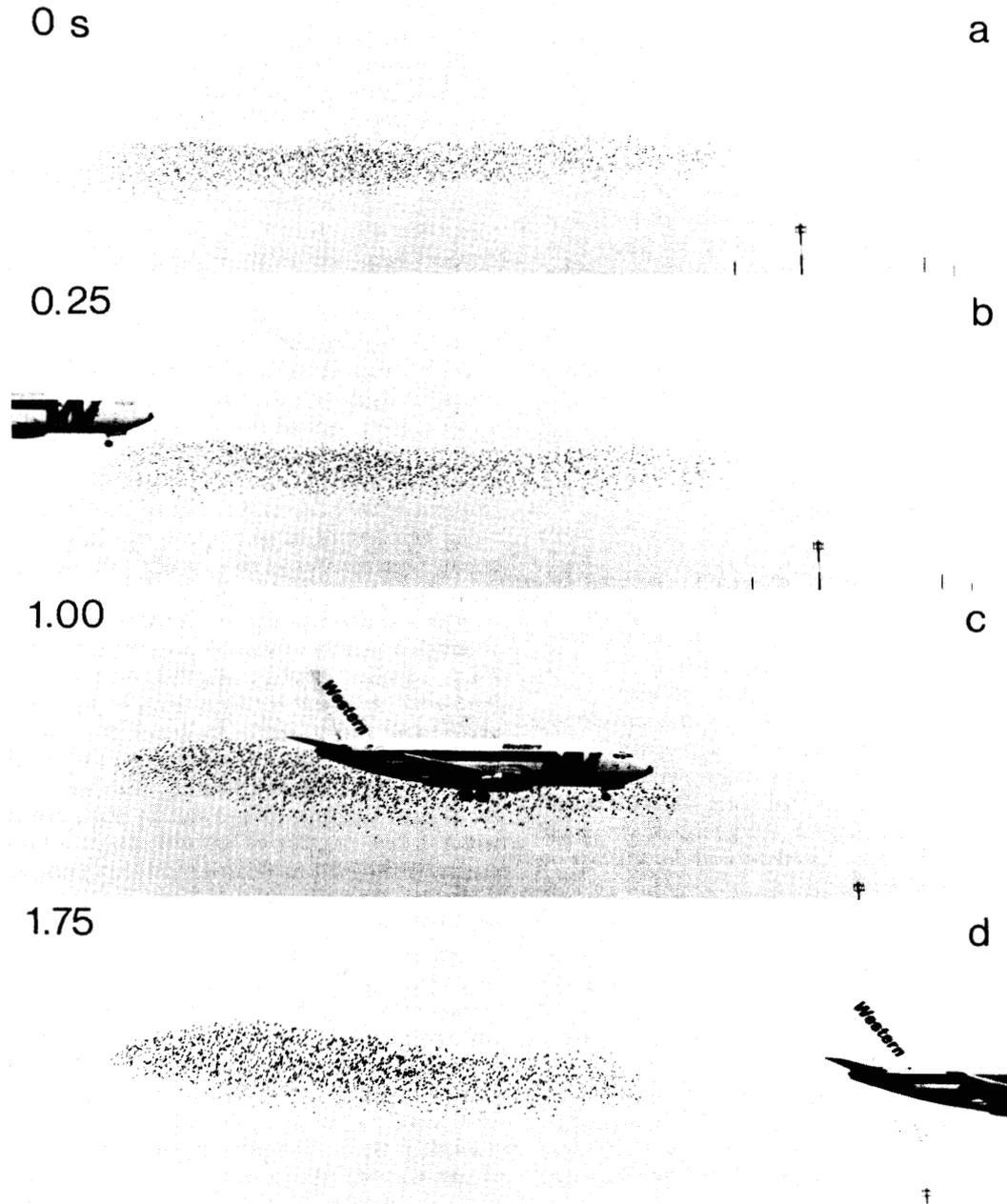


FIG. 3. Sequential photographs of a flock of starlings, *Sturnus vulgaris*, before, during, and after passage of a turbine-powered aircraft within an estimated 100 m. Total elapsed time is 1.75 s. The flock appears to shorten in length and become somewhat deeper (frames *a*, *b* to *c*, *d*). Bird density increased slightly (see text). This reaction to an approaching aircraft is similar to that seen when a natural predator approaches and exemplifies the predator-prey interactions simulated here.

interactions between aircraft and small flocking birds are a first approach to investigating such interactions. The approach may also be of value in other contexts, to be discussed below.

Flocking behavior characterizes many species of small birds inhabiting relatively open environments, e.g., fields, deserts, seashores, and marshes. Occurrence in flocks while feeding, resting, loafing, or roosting has been ascribed to a variety of functions, including increased time available for activities other than predator surveillance (Barnard 1980; Goldman 1980; Jennings and Evans 1980), more effective detection of predators (Pulliam 1973; Powell 1974; Siegfried and Underhill 1975; Lazarus 1979) and the "confusion effect" that large numbers of closely spaced "flashing" prey, moving synchronously might have on the ability of predators to single out and capture

individual flock members (Hamilton 1971; Vine 1971; Davis 1980; Potts 1984). These effects may be important in interactions between small flocking prey and single predators such as raptors (e.g., peregrine falcons). However, they are probably less important when the predator is much larger than individual prey, has a very high relative approach velocity, and occurs in groups itself.

Although assumptions and conventions of the model reported here simplify predator-prey interactions as they might occur in the field, the predators we have modelled are identical with actual engine frontal areas, and in some respects (e.g., speed) to natural predators as well. Similarly, the prey modelled are nearly identical with real prey, particularly dunlin. The results of this study support many of the theories concerning the advant-

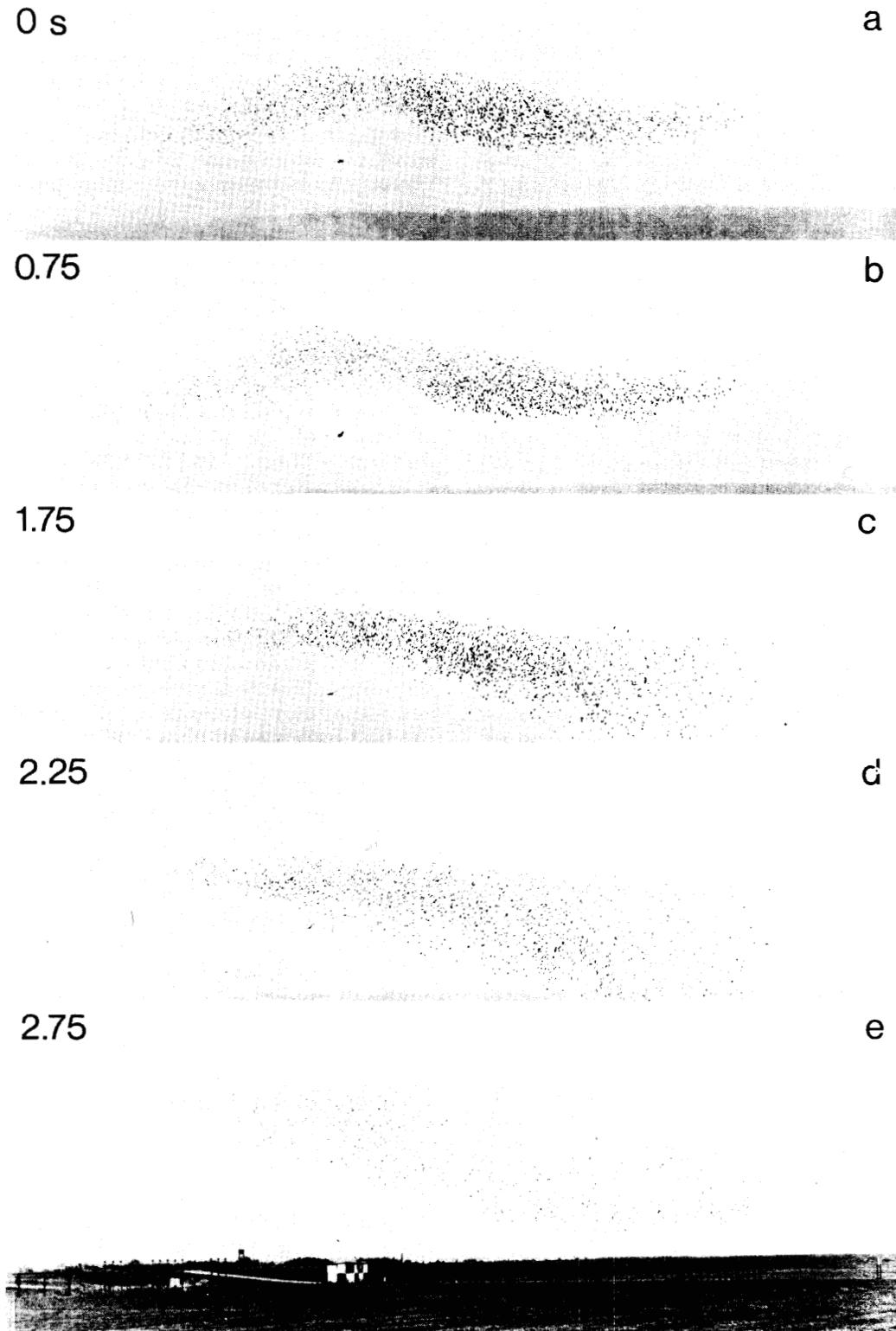


FIG. 4. Sequential photographs of a flock of starlings, *Sturnus vulgaris*, reacting to an approaching, but not pursuing, marsh hawk, *Circus cyaneus* (darker larger object to left of centre under the flock). Total elapsed time is 2.75 s. The hawk is flying from left to right (frame *a*), begins to turn away from the camera towards the distance (frames *b*, *c*), and continues around to the left (frames *d*, *e*), becoming obscured behind the flock in frame *e*. In frames *a* and *b*, the starlings form an avoidance arc over the hawk and appear denser immediately in front of it. As the hawk turns away (frames *b* and *c*), the flock expands, becoming less dense (frames *c*–*e*). This sequence of photographs was taken on the same day, at the same location, and following the sequence presented in Fig. 3. It is not known whether any of the individual starlings are the same in both photographs.

ages and disadvantages gained by individual prey forming aggregations in open environments (Brock and Riffenburgh 1960; Olson 1964; Hamilton 1971; Vine 1971; Major 1978), even when the predators are man-made and grouped, and behavioral factors such as "confusion" of predators by prey are not relevant. Interactions resulting in captures did not occur in all simulations as they would have if the prey have been uniformly distributed. Although a relatively large number of prey were captured when there was a collision, they represented less than 3–4% of the total number of prey in each simulated flock.

Our simulations represent the first investigation of the impact that predators, capable of consuming multiple prey simultaneously, have on a flock of small birds once it is located and "attacked." Differences in capture success as a function of predator group size and configuration were not great in the simulations reported here. When only a single predator was successful (primarily because of the bearing angle between the flock and predator disc 1 chosen), the larger predators (linear array) had a greater expected number of captures than the smaller ones (triangular array), all else being equal. Only a single predator captured birds in the flock angle of elevation, initial distance, speed, height, shape, volume, size, and density, and predator speed and angle of elevation simulations. When multiple predators were successful (flock bearing, lateral displacement, and size simulations for the linear array; flock bearing, angle of elevation, lateral displacement, and size and predator speed and angle of elevation simulations for the triangular array), their alignment in a cluster (the triangular array) resulted in a greater total expected number of captures. To put this another way, if the predators were tightly clustered around the first predator, the additional predators were more likely to capture prey and the total number of prey captured increased. The high relative speed and invariant trajectory of the predators modelled would account for these results. One might expect, however, that in a dynamic interaction the contact of a flock by one of a group of predators linearly aligned could result in all predators forming a clustered group. This has been suggested for aquatic predators observed to move through the environment in an echelon or linear configuration; the group coalesces upon the individual(s) actually locating prey (e.g., Partridge et al. 1983).

Qualitative field observations and unofficial records maintained by the Vancouver International Airport manager indicate that dunlin may be more vulnerable than starlings to aircraft. Differences in antipredator behaviors of the two species may be responsible, rather than relative abundance, which is similar when dunlin are seasonally present. When pursued by natural predators, dunlin flocks coalesce into tight spheres or ellipsoidal shapes (with reduced interbird distances and increased density) as they perform high speed, straight-line flight and protean maneuvers. Faced with approaching aircraft, whether landing or taking off, dunlin perform these same maneuvers. In contrast, starlings with their loose flock organization and densities (Major and Dill 1978) appear to rely more on maneuvers to evade rather than speed to outdistance predators in such situations. Therefore, behaviors resulting in dispersion and evasion would appear to be more appropriate for small flocking birds than coalescence when interactions with turbine aircraft occur. The responses by prey species in the field to turbine aircraft indicate that there may be some inflexibility in the prey's antipredator repertoire, even though that repertoire may be quite varied.

#### *Aquatic predator-prey interactions*

Some types of interaction between predators and prey in aquatic environments appear remarkably similar to those simulated here (Major 1978). Aquatic invertebrates can occur in densities of thousands or tens of thousands per cubic metre (Hamner and Carleton 1979; Drenner and McComas 1980; Byron et al. 1983; Hamner 1984; W. Dolphin, Boston University, personal communication). Aquatic predators that prey on planktonic species that form groups (or at least dense patches) are orders of magnitude larger than their individual prey, although the prey aggregations may be larger than a single predator. The predators also have high relative approach velocities (e.g., filter-feeding fishes or mysticete cetaceans compared to zooplankters).

The simulations reported here indicate that tightly grouped predators increase the total number of prey captured in comparison to single or linearly aligned predators. Such behavior would be particularly advantageous if the prey attempted to disperse when attacked, and grouped predators were able to concentrate them. This may help explain recent observations of the behavior of some humpback whales (*Megaptera novaengliae*) that cluster in groups when feeding on fish and crustacean prey near or at the surface in both northwestern Atlantic and southeastern Alaskan waters (Jurasz and Jurasz 1979; Hain et al. 1982; W. Dolphin, personal communication). Other studies (e.g., Radakov 1965; Neill and Cullen 1974; Major 1978) have demonstrated that grouped predators attacking grouped prey have higher capture success than single predators hunting alone. However, in these reports the predators' increased success resulted when prey groups were broken up, and individuals became isolated and vulnerable.

It is interesting to note that humpback whales are also known to produce streams or clouds of bubbles around, under, or near schools of prey (Jurasz and Jurasz 1979; Hain et al. 1982). This behavior has been hypothesized to assist in herding and concentrating prey. Individual and tightly clustered groups of these cetaceans then attack the prey.

#### *Applied examples*

From a practical viewpoint interactions between small flocking birds and aircraft have implications related to aircraft engine design and operations around airfields, since small flocking species do pose a hazard to aircraft, particularly during landings and takeoffs (Canadian Wildlife Service 1971; Blokpoel 1976). Although the aircraft engines simulated here captured relatively small numbers of birds, even these numbers may produce hazardous conditions. Modification of aircraft operations (e.g., timing of landings or takeoffs) when flocks of birds are known to be in the vicinity may be a relatively simple way to reduce the number of collisions. Such techniques are employed at airfields together with lights on aircraft to increase their visibility. In addition cracker shells and trained falcons have been used to scare birds from airfields.

The interbird capture time results reported here provide information about impact rates on turbine rotor blades, which have been known to break apart causing further damage to the engine. Such information could provide a basis for engine rotor blade design modifications and the use of stronger materials to withstand multiple impacts by small flocking birds.

Fishing and plankton sampling nets have largely evolved through trial and error. In some instances the target species sought are the same species preyed upon by the natural aquatic predators previously mentioned. Studies to improve the effec-

tiveness and efficiency of these nets have focused on reactions of single individual prey to nets in a two dimensional environment (Barkley 1964, 1972; Clutter and Anraku 1968; Murphy and Clutter 1972; Laval 1974; Wiebe et al. 1982), although Barkley (1972) does discuss prey avoidance behavior resulting from a reaction to other swarm members, rather than directly to an approaching net. To calibrate net efficiency and to calculate prey densities, population structure and avoidance behaviour, either identical or dissimilar nets (frontal areas) are deployed side by side in the same plane, perpendicular to the axis of travel. Because avoidance behavior of the prey organisms in their three-dimensional environment is not well understood, the use of techniques such as those employed in the present study, together with ideas for sampling such as those suggested by Wiebe et al. (1982), may produce more informative results about densities of planktonic organisms, some species of which are prey to large filter-feeding vertebrate predators.

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