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STRUCTURE OF TURNING IN AIRBORNE ROCK DOVE (*COLUMBA LIVIA*) FLOCKS

HAROLD POMEROY[1] AND FRANK HEPPNER
Department of Zoology, University of Rhode Island, Kingston, Rhode Island 02881, USA

ABSTRACT.—We describe a nonstereo, three-dimensional photographic technique to study the turning movements of flocks of semidomestic Rock Doves (*Columba livia*). The method permits sequential examination of an individual's position and flight path. The birds in flocks we studied with this technique did not maintain fixed positions. Birds continually repositioned themselves during a turn. Such repositioning of individuals may be more significant in the predator-evasion function of cluster flocks than for aerodynamics. *Received 8 February 1991, accepted 13 January 1992.*

THE WHEELING and turning maneuvers of birds flying in coordinated cluster flocks are commonly observed phenomena (Heppner 1974). The advantages incurred by birds within an organized flock structure may include aid in location and efficient exploitation of food (Murton 1968, Krebs 1973), detection of predators (Powell 1974, Siegfried and Underhill 1975, Kenward 1978), and use of neighbors as a physical screen from danger (Pulliam 1973, Treisman 1975).

A flock's chance of detecting an approaching predator may be greater than that of a single bird, and flock members may additionally derive protection from predators by the juxtaposition of neighbor's bodies between themselves and the predator (Pulliam 1973). Williams (1964) suggested that schooling behavior in fish arose from a kind of defensive hiding in which a threatened fish placed itself among other fish. Hamilton (1971) contended that an animal with nearby neighbors would have a smaller domain of danger. The selfish advantage to those individuals who sought cover by staying close to their neighbors might result in a tendency to aggregate. Hamilton's model related to two-dimensional groups. Parrish (1989), however, demonstrated that centrally located Atlantic silversides (*Menidia menidia*) in three-dimensional schools were at greater risk when their school was attacked by a black seabass (*Centropristis striata*).

Because birds on the periphery of a flock stand a greater risk of predation than solitary prey, it is to their advantage to peel away from the flock, exposing a new periphery (Pulliam 1973). Treisman (1975) argued that this behavior would tend to disband the flock, an argument that neglects the possibility that there may be a disadvantage to the first individuals to leave a flock. This disadvantage could be two-fold. Flocks are thought to offer passive structural protection from attack (Tinbergen 1951, Mohr 1960, Charnov and Krebs 1975). Individuals that leave the flock would lose this advantage, although the loss would not be confined to those who leave first. As birds leave the flock, they would become the odd prey item in the vicinity of the predator, exposing themselves to increased hazard from predators (Mueller 1971).

Two-dimensional analyses of certain structural attributes of flocks have been attempted using both radar (Williams et al. 1976) and photographic techniques (Miller and Stephen 1966, van Tets 1966, Nachtigall 1970, Gould and Heppner 1974). Dill and Major (1977) made the first analysis of the internal three-dimensional structure of cluster flocks. Their technique involved single, stereophotographic samples of many different flocks of European Starlings (*Sternus vulgaris*) and Dunlins (*Calidris alpina*). Although useful for establishing the internal structure of airborne flocks for any one instance, their method is not applicable to investigation of flock dynamics.

Breder (1976) presented a detailed model of the optimum geometric relationship between individuals in schools or flocks in the polarized (following parallel paths of motion) state. He noted that, because of the need for some type of locomotion by group members, it is necessary that a certain amount of space be maintained by each individual (Breder 1976, van Olst and Hunter 1970). Each individual, and a spherical

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[1] Present address: Academic Computer Center, Roger Williams College, Bristol, Rhode Island 02809, USA.

shell of space around it, is considered a unit sphere, and flocking or schooling represents a packing together of these spheres.

Davis (1980) made qualitative observations of mobility of individuals in Dunlin flocks, but his technique did not permit the three-dimensional tracking of individuals. Okubo (1986) noted that quantitative studies of the movements of individual animals in a group had been made only in invertebrates. We describe a method for such analysis in free-flying vertebrates and examine the structure of turning movements in coordinated flight flocks of Rock Doves (*Columba livia*).

METHODS

We photographed the flight-flocking behavior of a flock of 21 Rock Doves of the Birmingham Roller strain over a five-week period during the summer of 1980. Filming was done only on clear days when wind speeds did not exceed 18 ± 1 $\mathrm{km \cdot h^{-1}}$ (measured with a hand-held anemometer).

Although all 21 birds were released from their loft for each filming, a subgroup of 12 to 16 birds usually formed a cohesive cluster formation. The flocks remained airborne in the immediate vicinity of their loft for approximately 1 h. Birds not flying with the flock perched on the roof of the loft and were identified easily. We were able to identify individual birds within the airborne flocks because of their unique color patterns.

We took simultaneously exposed negatives of the airborne flocks with two identical fixed-position cameras. The 35-mm single-lens reflex (Topcon) cameras were equipped with motor drives and factory-matched 58-mm lenses. The factory-matched motor drives were connected to a common electrical control unit so that both cameras fired (single-frame rate). A premise basic to the study was that the negatives produced by the two cameras were exposed at exactly the same time. To test for synchrony of film exposure, the cameras were mounted in tandem such that they both faced the screen of a high-speed digital-readout timing device (Berkeley model 500B). Shutter speeds of both cameras were set at 1/1,000. The cameras were activated electrically from the common control unit at 650-msec intervals until the ends of the 36-exposure rolls of films were reached. Analysis of the exposed negatives indicated that the two cameras fired within 2.0 ± 1.4 msec, and the time period between firing remained 650 msec ± 1.4 for the entire 36 frames.

Cameras were mounted on tripods, and aligned initially with laser transits such that the intersection of their optical axes formed an angle of 90°. When viewed from above, the cameras would be located on opposite ends of a diagonal that bisected a square 60.80 ± 0.01 m per side. Benchmarks set in concrete permitted accurate positioning of cameras in subsequent sessions. Both cameras pointed at a common third corner of the square. The resulting area of overlap of the visual fields of view of the cameras approximated a 1,000-$\mathrm{m^2}$ square. The cameras were activated from a remote position when the flock was within the field of overlap. The filming area and immediately adjacent loft were located in a 20-ha turf farm.

Photographic samples of the flocks were taken at 650 ± 2 ms intervals. A 16-mm movie camera, used in addition to the still cameras, provided continuous data on the positions of birds. The movie camera was mounted in tandem with one of the 35-mm cameras so that both yielded similar pictures of the flock. A small lightbulb, wired in series with the control mechanism that synchronized the motor drives, lit each time the still cameras were activated, and made it possible to mark the frames of movie film when the still cameras fired. The movie camera ran at a rate of 24 $\mathrm{frames \cdot s^{-1}}$, resulting in a sequence of 16 frames of movie film between each consecutive pair of still-camera photographs. The more detailed information obtained from the movie film was helpful in tracking the paths of specific birds within the flock.

Developed film rolls were viewed at 10× through a modified microfilm reader (Eastman Kodak model C) to check the quality of the negatives. Film-pair sequences found usable were printed (8- by 10-inch RC paper).

As the exact magnification involved in making each print was used in the analytical procedure for calculating the positions of birds, a nonstandard printing procedure was required. The negatives were held in place in the enlarger between two thin plates of achromatic glass, rather than by a standard negative holder. This allowed for the entire 24 mm by 36 mm area of the exposed negative and the area around it, which included the sprocket holes in the film, to be printed on the RC paper. The actual width of the sprocket holes in 35-mm film is 1.96 ± 0.05 mm. Measurement of the image of the sprocket hole in prints proved the most convenient method of determining the enlargement involved in making the prints.

Image analysis was done by mounting photographic prints from the negatives on a light table and measuring each bird's position on the print with digital readout calipers (Brown and Sharp DigiCalc). The position of the head of the bird on the print was used in making measurements. The orientation of birds relative to the cameras sometimes necessitated estimating the approximate point of the head of a bird on a print.

Absolute position.—Information derived from the prints was first used to establish where in three-dimensional space each bird in the flock was located each time photographic samples were taken. A Cartesian-coordinate system was defined for this point-in-space analysis. The X- and Y-axes of the system were perpendicular and crossed at the point of in-

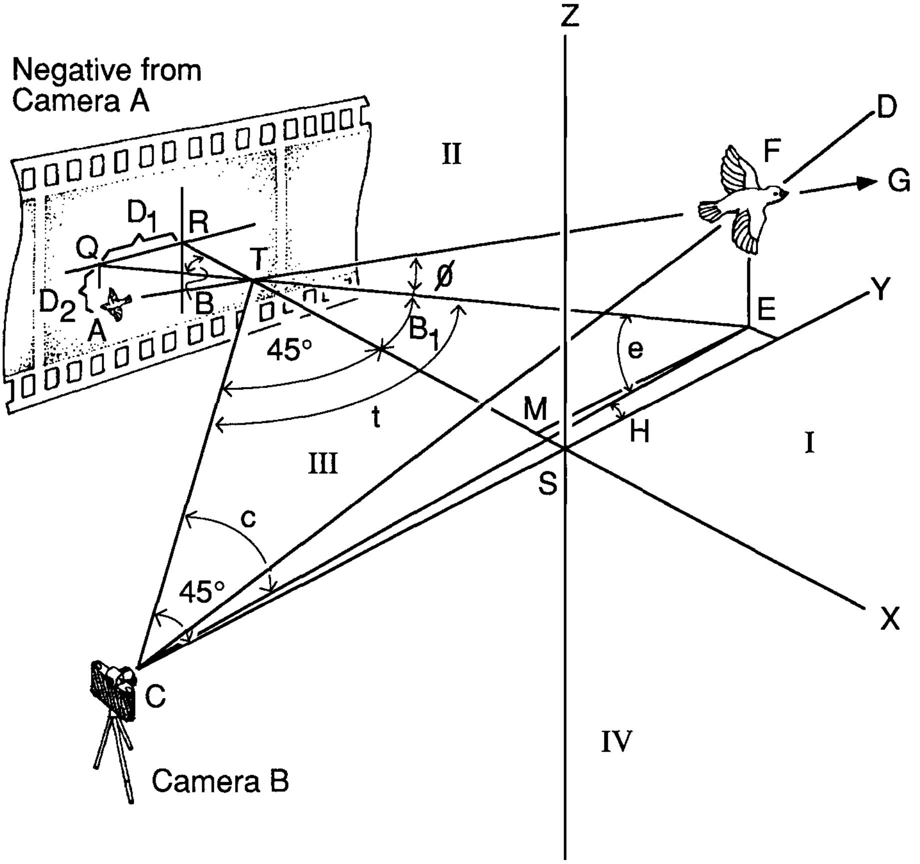

Fig. 1. Calculation of positions of birds in three-dimensional space. Image of bird at point *F* forms on negative of camera *A* to yield distances D_1 and D_2. These distances are used in a series of geometric calculations to locate point *F* (see text for full explanation of calculations).

tersection of the optical axes of the two 35-mm cameras. The *XY*-plane was parallel with the ground. The Z-axis, or vertical axis, of the system was defined as perpendicular to the *XY*-plane. The elevation (Z-axis), and the bird's displacement along the horizontal grid system (*XY*-plane) were the real-space coordinates of the bird. Real-space coordinates were calculated for each bird in the flock for every point in time at which the flock was photographed. For the computer program developed to determine the position of a bird, we used the horizontal and vertical deviations of a bird's image from the center of a negative as the basis for all calculations (Fig. 1).

The position of a bird on a negative from camera *A* can be used to locate that bird along a line originating and extending from point *T* (the optical center of the lens) to point *G* at infinity. The bird could be anywhere along line *TG*. Line *TG* is determined as follows: The horizontal displacement (distance D_1) of the image of the bird's head from the center of the negative is measured to yield the length of side *QR* in triangle *QRT*. Side *RT* of the triangle is the focal length of the camera lens when focused at infinity (58 mm). Angle *B* in right triangle *QRT* can be expressed as $\tan^{-1}$ (*QR*/*RT*). Triangles *QRT* and *MET* are corresponding right triangles, such that angle B_1 in triangle *MET* is equal to angle *B* in triangle *QRT*. Angle B_1 in triangle *MET* defines the horizontal displacement of line *TG* on the *Y*-axis. With this information only, the bird could be in quadrant I or II.

The same process is used with data from camera *B* to locate the bird along line *CD*. The intersection of lines *TG* and *CD* defines point *F*, which will be the position of the bird in three-dimensional space. It now becomes necessary to determine the *X*-, *Y*-, and Z-coordinates of point *F*.

In the example shown in Figure 1, the photograph from camera *B* shows that the bird is left of the center line (Z-axis). In the view taken from camera *A*, the bird is also left of the Z-axis, placing it in quadrant II of the *XY*-plane. Lines *FE* (Z-coordinate), *ME* (*Y*-coordinate), and *MS* (*X*-coordinate) must now be determined.

Triangle *TEC* in the *XY*-plane connects the optical

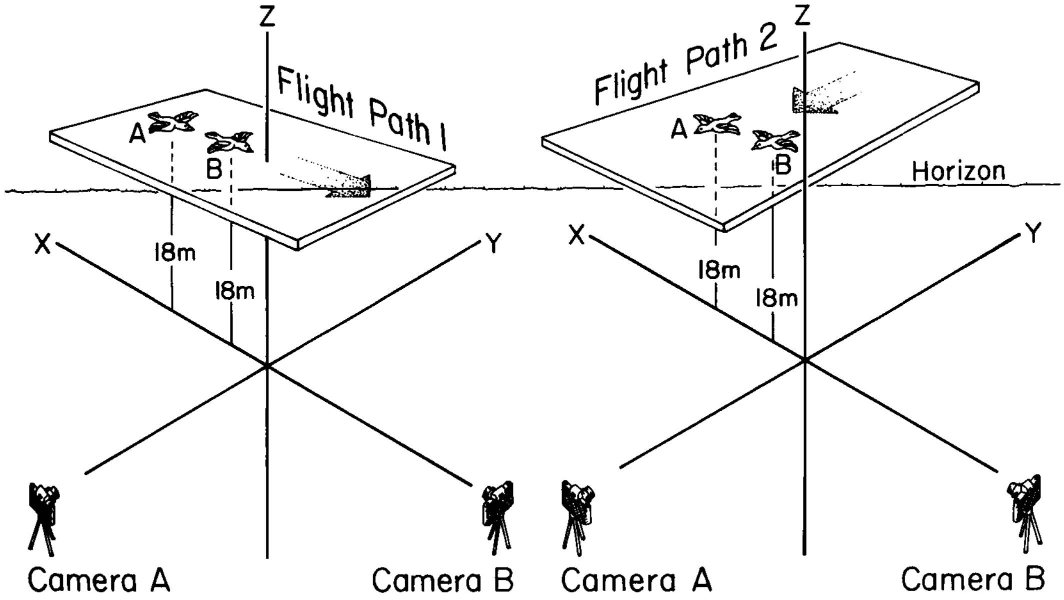

Fig. 2. Effect of flight path upon relative positions of birds within flock. On left panel, a level flight path in which bird *B* is directly in front of bird *A*. On right panel, a turn is depicted. Although absolute positions are the same, bird *B* in right panel is now to left of *A*.

center of the lens of camera *A* (point *T*), and of camera *B* (point *C*), with point *E*, which is the projection of point *F* onto the *XY*-plane. Side *TC* of triangle *TEC*, the distance between the cameras, is a measured distance. Angle *t* (given by $\angle B_1 + 45°$), angle *c* (given by $45° - \angle F$, which is the angular deviation of *CD* from the *Y*-axis as determined from photographs taken by camera *B*), and angle *e* (given by $180° - [\angle t + \angle c]$) are all known. All internal angles and side *TC* of triangle *TEC* are now known. Thus, side *TE* can be determined as

$$TE = [(TC)\sin(\angle c)]/\sin(\angle e). \quad (1)$$

The position of the bird along the *Y*-axis (side *ME* of right triangle *MET*) is given by $(TE)\sin(\angle B_1)$. The elevation of point *F* above the *XY*-plane can be calculated by determining the length of side *EF* of right triangle *TEF*. Side *TE* and angle ϕ of the triangle are known. Distance *EF*, the elevation of point *F*, can be expressed as $[\cos(\angle\phi)]\ (TE)$. The displacement of the bird along the *X*-axis (side *MS*) is determined as follows. The distance from the optical center of the lens of camera *A* to point *S* is constant ($TS = 60.80$ m). Side *TM* of right triangle *MET* can be calculated as

$$TM = (ME)\,[\tan(\angle B_1)]. \quad (2)$$

In this example, where the bird is in quadrant II, distance *TM* must be subtracted from 60.80 to yield *MS*.

The *X*, *Y*, and *Z* Cartesian coordinates of all birds in the flock were determined for every time at which photographic samples of the flock were taken. Coordinate positions of each possible pairing of birds were used to calculate distances between flock members using the formula:

$$D = [(X_R - X_N)^2 + (Y_R - Y_N)^2 + (Z_R - Z_N)^2]^{0.5}. \quad (3)$$

Subscripts *R* and *N* in the formula refer to the reference (*R*) and neighbor (*N*) birds. Each bird in the flock was analyzed in turn as the reference bird for every time at which the flock was photographed. Distances between each reference bird and all other birds in the flock were calculated to yield a series of values for first-nearest neighbor, second-nearest neighbor, through *N*th-nearest neighbor. Data for each of the neighbor-distance categories, and the associated mean values, were plotted over time to represent graphically the structure of the flock.

Mean separation distance between all flock members was calculated for all times at which the flock was photographed. This distance is the average of all unique combinations of between-bird distances within the flock. Nearest-neighbor distance is not sensitive to fragmentation of a flock into subgroups. Mean separation distance is sensitive to such changes in structure and, thus, is a measure of flock compactness (Hunter 1966). Plots of changes in the relative values of these two parameters over time were used to study internal flock structure.

A field test was performed to determine empirically the accuracy of the photographic and digitizing methods employed for each trial. A three-dimensional test "flock" in which the distances between "birds" and angular relationships between "birds" were known

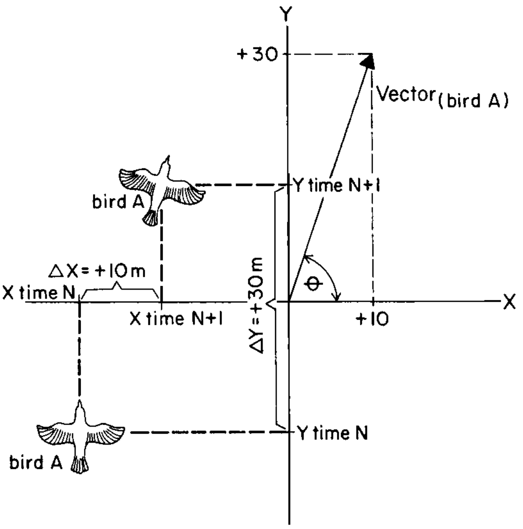

Fig. 3. Calculation of horizontal component of flight path of flock. Bird *A*, as viewed from above at two points in time, is shown to have turned to right. Displacements along *X*-axis (ΔX) and *Y*-axis (ΔY) are used to determine angles and, thus, flight vector of bird *A*. Sums of all *X*s and *Y* s were used to find angle θ for flock as a whole.

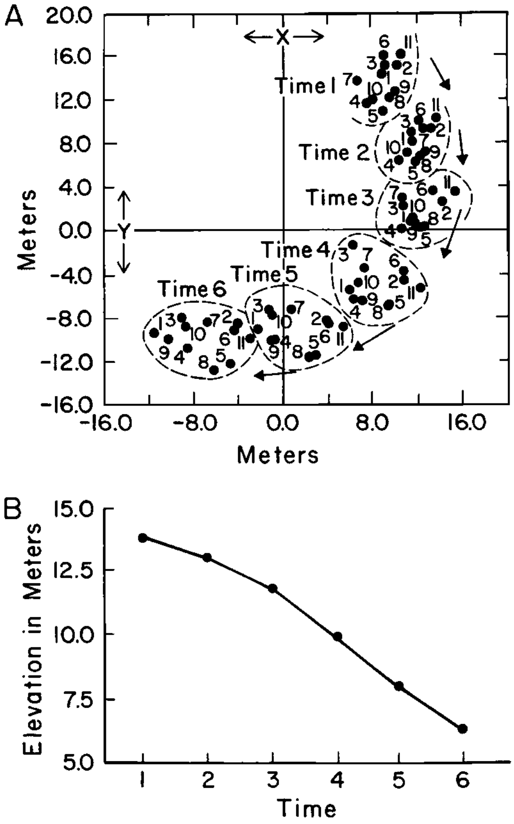

Fig. 4. Summary information on flock movements over time. (A) Flock in release 7 as seen from above for each point in time at which photographs were taken. Numbers within dotted lines denote individual birds, whose positions are shown with dots. Deployment of birds in horizontal plane is readily seen. Arrows indicate mean direction of travel of flock. (B) Changes in elevation of geometric center of flock occur as flock travels.

(121.9 cm, 30.0°) was constructed from wood dowels and Styrofoam "birds." The test flock was suspended from a helium-filled balloon. Two assistants on the ground used tether lines to "fly" the apparatus through the filming area. Analyses of the sequence of photograph pairs taken of the model provided an estimate of the error term for the experimental method. The calculated distances between "birds" and angular relationships between "birds" differed from the actual measured distances and angles by ±2.6%. This test was repeated before each filming session with flocks.

Relative position.—The real-space positions of birds were used in a second step of the analysis to assign positional relationship to birds in the flocks. The terms right, left, above, and below were defined as a function of the flight direction of the flock (Fig. 2).

Changes in the positions of birds over time were used to determine continually the direction of travel of the flock. The three-dimensional coordinates of birds at two successive time periods were used to determine the birds' displacement along the *X*-, *Y*-, and *Z*-axes. The horizontal and vertical components of the flight path of the flock then were determined using circular statistical methods described by Batschelet (1965).

The original Cartesian-coordinate system was shifted in several steps to obtain relative positions of birds within the flock. The first shift of the axes adjusted for the horizontal component of the direction of travel of the flock (Fig. 3). The *XY*-plane was rotated on the *Z*-axis so that the *X*-axis was parallel to the horizontal component of the flight direction of the flock. The axes were then adjusted to the vertical component of the flock's flight path. The axis system was rotated on the *Y*-axis so that the *XY*-plane was inclined or declined to correspond with the vertical component of the flight path of the flock. The last step of adjustment involved placing the rotated axis system at the geometric center of the flock.

A rotated and centered system of axes was made for all but the first time period in the series of photographic samples. The positions of birds at time (T + 1) were recalculated in reference to a coordinate system defined by the flight path of the flock from time T to time (T + 1). The resulting series of plots of birds' relative positions on the *XY*- and *XZ*-planes (flock as viewed from above and from side, respectively) yielded information on each bird's position within the flock relative to other birds in terms of right, left, above, and below. These plots were used to ascertain whether the integrity of the positional relationships between birds was maintained as the flock flew through the air.

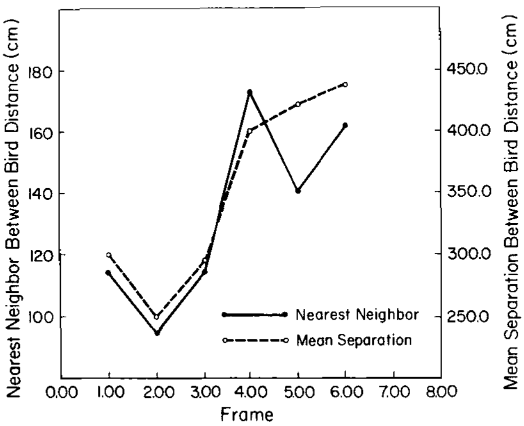

Fig. 5. Changes in values for mean separation distance, and mean distance to first nearest neighbor for six time periods in release 7.

RESULTS

The turning and wheeling maneuvers of flocks flying around their loft were photographed on seven occasions. All birds housed in the loft did not fly with the airborne flocks during the filming of each release. For different filmings, therefore, the composition of individuals and total number of birds present in the flock varied. A complete analysis of one filming will demonstrate the types of information provided by the methods developed for the study. An analysis of all flocks studied is presented in Pomeroy (1983).

The horizontal spread of the flock as seen from above at each point in time is readily seen (Fig. 4A). The time period between photographic samples of the flocks remained constant at 650 msec, so that the relative distances traveled by birds between times can be seen. The elevation of the geometric center of the flock was plotted at each of the six time periods (Fig. 4B). In this release the flock was executing a right turn of approximately 90°, while losing altitude, and was accelerating.

First-neighbor pairings and associated separation distances, as well as the mean distance to each neighbor of each bird, were calculated for the six time periods (Fig. 5). As indicated by mean separation distances, the flock became more compact from time 1 to time 2, then expanded. From time 4 to time 5, the flock continued to expand, while at the same time the average distance to the first-nearest neighbor decreased. This combination of changes in the two parameters is an indication of the formation of nearest-neighbor pairs of subgroups within the expanding flock.

More complete information on flock structure during each portion of release 7 may be obtained from plots of all neighbor distances within the flock and interpretation of neighbor-distance plots with reference to: (1) the height and slope of the line connecting mean neighbor distance; (2) the step versus smooth linear increase in distance to neighbors; and (3) the distribution of distance values within the neighbor classes (Fig. 6A). There is a near linear increase in nearest-neighbor distances ($R^2 = 0.78$), indicating no subgroups or clumps. The distribution of values within each neighbor class suggests that no stragglers existed at this time.

The flock was compact from time 1 to time 2, and then expanded (Fig. 5). The dotted lines (Figs. 6B through 6D) are a trace of the solid line connecting the mean neighbor distances at time 1. This dotted line appears as a reference so that changes in the distribution of neighbors can be seen more readily.

The changes over time in the line connecting the mean distance to neighbors could take several forms representing either an expanding or contracting flock structure. The line could remain linear, with a change in slope. An increase or decrease in all neighbor distances could occur, resulting in a line that is parallel to the solid line of time 1, but representative of different distance values. The third alternative is for the original line to exhibit one or more large changes in slope, indicating a step increase in distance to neighbors characteristic of subgroups or clumps.

The flock became more compact from time 1 to time 2 due to a decrease in distances to all neighbors (Fig. 6B). The occurrence of high values in the distributions for third through tenth neighbor (Fig. 6C) indicates a group of three birds broke away from the main body of the flock. The only distribution of birds in a flock that could be inferred from the plot (Fig. 6C) would consist of three birds that were close to each other so that the distances to first and second neighbors had no high values, but were relatively distant from the rest of the flock. Their distances to third through tenth neighbors, thus, would appear as the high values in the classes. This suggests that the flock has split into two large subgroups.

The mean headings of the flock in both the horizontal and vertical planes were calculated for each but the first sample, and used to establish birds' relative positions within the flock. The data were used to generate the two views of the flock for each time period (Fig. 7). The plot on the top shows the flock as viewed from above. The plot on the bottom is the same flock viewed from the side. Note that the axes have been centered at the geometric center of the flock for each point in time, with the *X*-axis pointing in the direction of travel of the flock.

Without reference to the relative positions of birds, this plot confirms that: (1) the flock is expanding over time; (2) the expansion is more horizontal than vertical; and (3) the pattern of expansion is into nearest-neighbor pairs and clumps as predicted by previous plots.

Examination of changes in the relative positions of specific individuals (Fig. 7) suggests considerable movement of birds within the flock. Some birds (9 and 10) maintained the same relative position within the flock over time, while the positions of other birds (2, 6, 11 and 5, 8) rotated counterclockwise through the flock structure. In all flocks, 75.6% ± 12.5 SD of all birds ($n = 7$) were in a different quadrant of the flock at the end of a turn than the one in which they started.

The rotation within the flock of the relative positions of birds may be explained through inspection of the flight paths of birds. The flight path of each bird was a unique arc through space. Those birds, such as individuals 6, 2, and 11, whose flight paths were the same maintained positions close to each other over time. Birds 5 and 8 flew together on a flight path that described a different arc than that of birds 2, 6 and 11. The redistribution of birds within the flock (Fig. 7), thus, is due to the fact that different birds, or groups of birds, had flight paths

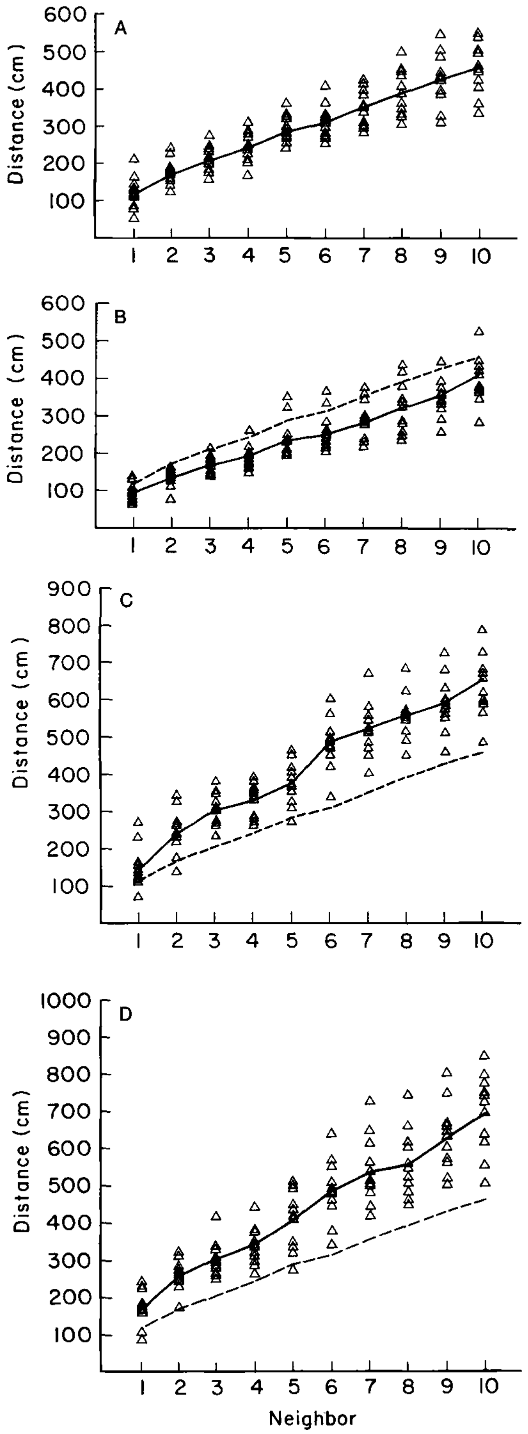

Fig. 6. Distances to first through *N*th neighbor within flock are plotted for selected time periods at which flock in release 7 was photographed. Neighbor-distance distribution shown for (A) time 1, (B and C) intermediate times, and (D) time 6. Solid line in ← each plot connects mean values of distributions. Dashed line in second and subsequent plots shows connected mean values at time 1 so that changes in distributions over time may be more readily interpreted.

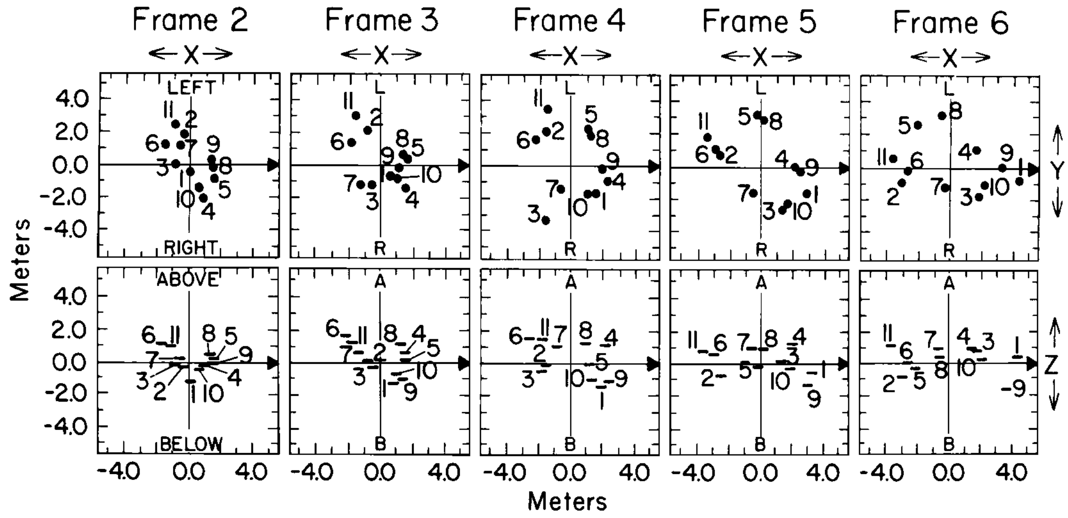

Fig. 7. Relative positions, shown from two viewpoints, of flock members in release 7 for five periods during which relative position could be calculated. Assigned numbers of birds are shown as seen from above (top plot) and as seen from the side (bottom plot). The *X*- and *Y*-axes have been centered at geometric center of flock in each plot. Arrow at right of *X*-axis indicates direction of travel of flock. For each plane, flock is visualized as moving within four quadrants formed by perpendicular lines centered at geometric center of flock.

whose arcs were either of different radii, or of similar radius but which originated at different centers. The latter situation would result in arcs which crossed and, thus, the rotation of the relative positions of birds.

Birds that continued to fly on a course so as to maintain positions close to each other are considered to be part of a closely-flying subgroup (CFS). One must monitor the positions of birds over a period of time to establish CFSs and, thus, no previous analyses of bird flocks have detected such associations. If one considers birds 2, 6 and 11 as a CFS during the six time periods in release 7, the previous graph analyses, which established clumped distributions of birds within the flock, indicated that these three birds were in a physical clump only during time periods 2 and 5.

DISCUSSION

Breder's (1976) model for organized groups of vertebrates states that no individual in the group has another individual to either side or directly above or below it. The spatial relationships between individuals in a single layer of such a packed group approximates a diamond shape (Wiens 1973). Three-dimensional analyses of the distribution of fish in schools have demonstrated this type of deployment (Cullen et al. 1965, Hunter 1966, Pitcher 1973). The applicability of the model to globular flight formation (Heppner 1974) is shown in Dill and Major's (1978) nearest-neighbor analysis of European Starling and Dunlin flocks.

This model restricts the potential directions of travel available to group members when the formation is turning. Breder (1976) noted that a tighter packing of individuals would require a more precise deployment of group members. With individuals distributed in a fixed geometric pattern, certain areas of the flock or school represent forbidden paths of direction of travel. These forbidden vectors would require too close a mutual approach of individuals while turning. The size and position within the group of these critical areas is a function of the density of the group. Thus, a group must expand to make a sharp turn and, as the group becomes more compact, the potential for individuals to redistribute themselves within the overall structure quickly diminishes. Hunter (1966) demonstrated this phenomenon in fish schools, noting that periods of high angular deviation in the headings of fish always resulted in an expansion of the school structure. Individuals in such a group would be more or less fixed into place for as long as the compact structure was maintained. A bird on the outside of such a structure would not be able to reposition itself to the center or "safe side" of the flock in response to a predator.

If the positions of birds within a flock were not fixed, birds could place themselves in specific parts of a flock, or at random positions, and attempt to relocate within the structure if the flock was attacked. Some degree of structural reorganization is common in responses of many flocks to a predator (Nichols 1931, Tinbergen 1951, Mohr 1960, Dill and Major 1978). The effectiveness of a fixed-position versus a variable-position strategy depends on the extent to which birds can move about within a turning and wheeling cluster of birds.

The mean distance to first-nearest neighbor for flocks in the present study (153.8 cm) is similar to that reported by Dill and Major (1978) for Dunlins (70.0 cm) and European Starlings (145.0 cm). Absolute distance to the nearest neighbor as a measure of the density or compactness of a flock is not sensitive to the length of the birds that are spacing themselves in the flock. One can take into account the length of the birds in a flock by computing the ratio of distance to the first-nearest neighbor to the average length of flock members. The range of values for the ratio in the present study goes from approximately 4:1 (which is close to the 3.25:1 ratio of the tightly packed Dunlin flocks) to 8.5:1 (which is slightly higher than the 7.1:1 ratio reported for European Starling flocks; Dill and Major 1978).

The polarized Dunlin and European Starling flocks exhibited the internal geometric construct predicted by Breder's (1976) model of optimum packing. This construct has been observed during many fish studies (Shaw 1978). The Rock Dove flocks of our study did not maintain a precise geometric construct, and did not seem to be affected by the limitations of movement of individuals within the structure, which Breder's (1976) model suggested. The flocks in many cases did maintain a compact structure while performing a turning maneuver. The following suggestions may explain the observed results.

The distances between fish in schools relative to the size of fish indicate that there is much less internal empty space in schools than in bird cluster flocks. Hunter (1966, 1969) and van Olst and Hunter (1970) demonstrated that spacing between fish in four species of jack mackeral (*Thrachurus*) was approximately equal to one-half the body lengths of individual fish. Pitcher (1973) and Cullen et al. (1965) also found nearest neighbors were about one-half a body length apart.

The greater amount of relative empty space in cluster flocks may be necessitated both by the medium in which birds travel, and their speed. The empty space makes it possible for birds to be in transit through the flock structure during times the flock is turning. High angular deviation in headings of fish in schools indicate a decrease in compactness, and a breakup of the structure so as to allow fish to negotiate a turn. The potential for birds to travel through the flock resulted, in many cases, in a more compact flock at the time of the highest angular deviation of headings (i.e. in turning).

Turns we recorded all were sharp, and seemed to involve a breakdown in any structure that may have existed prior to the turn. In contrast to a column turn, the flight paths of many birds approached or crossed during a turn. This particular aspect to the pattern of change in the deployment of birds may be significant in an analysis of leadership, if such exists, and the propagation of information throughout the flock.

A simple model of turning consistent with the data would involve all birds in a flock starting to turn at approximately the same time, and each bird describing an arc of similar radius originating at its position at the onset of the turn (Fig. 8). The plot shows that the crossing of flight paths of birds results in the counterclockwise rotation of their relative positions within the flock. Such a pattern of repositioning of birds within the flock was observed in all the flocks of this study. Not shown in the figure is the fact that the crossing of flight paths of unequal radius could bring birds together in physical clumps for a short time. This type of temporary association between birds also was observed.

There is probably less significance to the temporary spatial association of birds whose flight paths cross at one point in time than would exist for birds that tended to maintain parallel and proximate flight paths throughout the entire course of a turn. In all releases, some groups of birds continued to maintain positions close to

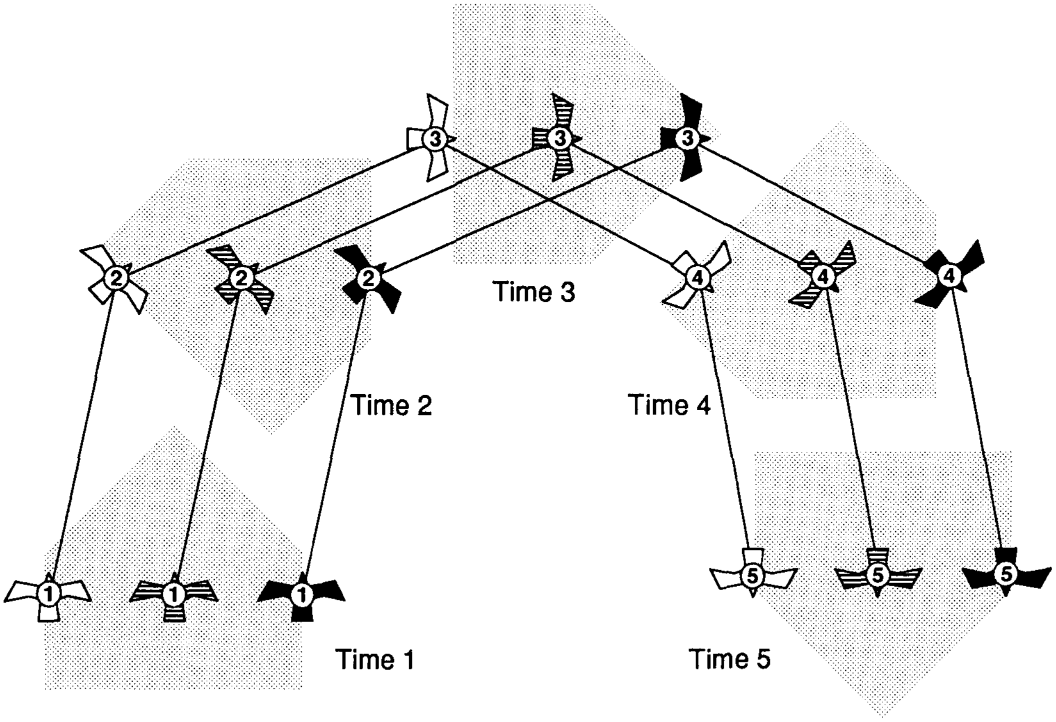

Fig. 8. Flight paths of two individuals traveling on either side of center of flock. During course of turn, all individuals follow arcs of equal radius. Distance traveled along an arc between time periods is same for all birds. Relative positions within flock of these individuals rotate counterclockwise over time. Note that flight paths cross.

each other as the flock traveled through the turn. If individuals were adjusting their flight paths to a few nearest neighbors rather than the central mass of the flock, a breakup of the flock into subgroups, as seen in several releases, would occur. Pairs or groups of birds within a flock that follow similar paths through space may be considered CFSs. In release 7, the CFSs were also distinct physical clumps because the flock was breaking apart. CFS in a flock that is compact and not expanding may not appear as distinct physical units within the overall flock structure.

This situation existed in release 2 (Pomeroy 1983). A group of birds originally on the outside edge of the flock relative to the turn, cut short. Another subgroup did not respond to the turn as quickly, and turned later and on a different arc than the first group. As a result, the flight paths of the subgroups crossed. There was a breakup of the original subgroups into two distinct CFSs. The crossing of the flight paths of the CFSs resulted in birds switching relative positions within the flock. Because the two CFSs were passing through each other, at no time did the flock separate into distinct physical clumps.

The maintained spatial association in CFSs could be the result of random paths, or it could result from pairs or groups of birds within a flock that respond to each other over time in adjusting their flight paths. The concept of individual response to specific neighbors has a basis in both fish schools and bird flocks. Hunter (1966) studied the communication of velocity changes in schools of jack mackeral. He demonstrated that responding fish may be quicker to sense alteration in a neighbor's behavior if the neighbor occupies a particular area of the visual field. Potts (1984) found that a wave of turning in Dunlins could propagate faster than the birds' reaction times. It is very common for pairs or small groups of birds to break away from and then rejoin cluster flocks, a situation that would occur if birds followed specific neighbors within the flock, resulting in pockets of response. Localized pockets of response have been observed to form within schools of fish that are turning (Shaw 1978).

A spherical flock structure involving relatively fixed positions of individuals would offer distinctively different advantages to peripherally and centrally located birds. Our study suggests that turning and wheeling cluster flocks are in a constant state of structural reorganization, and that adaptive strategies for reducing the risk of predation could be based on the phenomenon of relocation rather than on maintaining a fixed position in the flock (Hamilton 1971). A bird would not necessarily have to peel off from the surface of the flock (Pulliam 1973) to become separated from the flock. Any individual located in the center area of a flock could easily become a straggler, due to positional rotation of individuals in a turn.

The position in space at which a bird is located in relation to other birds in the flock may be a function of which bird or birds the individual attempted to follow and respond to in making adjustments to its flight path. This effect is compounded by the fact that with birds traveling at 25 $\text{km}\cdot\text{h}^{-1}$ and making a sudden, sharp turn, a slight delay in response could result in a very different arc of turning and could cause the responding bird to either leave the flock, or end up in an area of the flock distant from the bird to which it had responded.

The continual redistribution of birds within turning flocks has bearing on several current hypotheses of the aerodynamics of flocking behavior. It has been proposed that birds in flight formations could theoretically achieve an aerodynamic advantage by flying in the updrafts created by their neighbors (Lissaman and Schollenberger 1970, Higdon and Corrsin 1978, May 1979). Models that relate various three-dimensional flock structures to reduced induced drag to all members of the flock may not apply to flocks when flock members are turning in a manner described in our study. The aerodynamic models assume a maintained and specific geometric construct within the flocks. The crossing of flight paths and changes in flock compactness we observed indicate that birds could not long remain in the updraft segments of wingtip vortices from leading birds.

The birds within the flocks of Dill and Major's (1978) study were deployed in a manner that might result in an aerodynamic advantage to flock members. The flocks they filmed were in the process of traveling between roosting and feeding areas, or migrating through the study area. Birds of the same species respond to predators by flying in compact, turning and wheeling cluster flocks (Dill and Major 1977). Under the latter condition, the adaptive strategies of flocking may relate to each individual's ability to protect itself rather than aerodynamic advantages. It would seem very likely however, that birds can easily and rapidly switch from an aerodynamically advantageous flock formation to a flock configuration in which evasive maneuvers, staying with the group, and structural protection acquired from neighbors minimize the threat of predation. Probably the turning and wheeling flocks we observed are only one of the types of flocking behavior exhibited by birds that normally fly in a cluster formation.

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