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Three-Dimensional Analysis of Turning Within Airborne Bird Flocks

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THREE-DIMENSIONAL ANALYSIS OF

TURNING WITHIN AIRBORNE

BIRD FLOCKS

by

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ABSTRACT

The three-dimensional structure of airborne pigeon flocks was moni-
tored over time. Flocks changed both in overall shape, and in compact-
ness during the execution of turns. Flight speeds of the flocks were
sensitive to the vertical rather than the horizontal component of a turn.
The compactness of flocks did not seem to change in relation to speed
maintained during turns or sharpness of turns.

The cues to which birds responded in adjusting their flight paths
may be important in determining flock compactness. Birds within flocks
responded to each other's position and maintained positions close to
each other. In a flock groups of birds which maintained positions close
to each other were observed as a distinct physical clump of nearest
neighbors only if the overall flock structure was dispersed or was
expanding over time. Birds flying on very different flight paths were
occasionally observed to become temporary close neighbors due to the
crossing of the arcs describing the flight paths of the birds. Under
such conditions birds could possibly be detected as a physical clump of
close neighbors within the overall structure of the flock.

Birds in flock performed aerial flight maneuvers while maintaining
or increasing the compactness of the flock structure. The relative
positions of birds within the flocks were not fixed. The repositioning
of birds within the overall structure of turning and wheeling flocks
indicates that adaptive strategies for predator avoidance could be
based on a bird's ability to easily reposition within a flock, rather
than on the distinctly different advantages of maintaining a peripheral
or central location within the flock.

Behaviorally dominant and subordinate birds did not maintain specific positions within the airborne flocks. There was a tendency for birds of dissimilar dominance rank to be nearest neighbors within the airborne flocks.

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INTRODUCTION

An uneven distribution and relative scarcity of certain essential resources may promote and necessitate the gathering of birds into flocks to exploit resources. Flocking aids in the location and efficient exploitation of food (Short, 1961; Morse, 1970; Murton, 1968; Hamilton and Gilbert, 1969). Turner (1964) pointed out that imitiative foraging by birds in flocks would facilitate locating and switching to new food sources. Ward and Zahavi (1973) proposed that flocks act as information centers for food finding. Birds may gain from other flock members information on where (Krebs et al., 1972; Krebs, 1973) and what to eat (Greig-Smith, 1978; Murton, 1971).

The ability of individuals in flocks to harvest food sources more radily than an equal number of birds foraging individually has been attributed to the early warning function of flocking (Lazarus, 1978). Pulliam (1973) provided a simple calculation to show that a flock will have a greater chance of detecting an approaching predator than a single bird. The probability that at least one member of the flock will detect a predator before it sets within range of attack increases with the size of the flock. Since knowledge of danger can be rapidly transmitted to other individuals either passively by orienting and escape movements or actively by alarm signals, all members of the flock can take evasive action sooner than if they were alone or in a smaller flock. Lazarus (1977) termed this the early warning function of flocking to emphasize the importance of early detection in facilitating escape.

Many predators rely on surprise for their success and abandon an
attack once they have been detected by the prey (Rudebeck, 1951;
Kenward, 1978). Numerous studies using a measure of the time to take
flight in response to an approaching hawk-model have procided empirical
support for the early warning hypothesis. Powell (1974) found response
times to a predator shorter for flocks of ten Starlings than for
single birds. Siegfried and Underhill (1975) found that response time
in flocks of Laughing Doves declined as flock size increased within the
range of four to fifteen birds. Kenward (1978) observed that larger
flocks of Woodpigeons took flight at a greater distance from an approach-
ing tame Goshawk.

Lazarus (1977) measured the probability of detection of a predator
by different sized flocks using a trained Goshawk and an artificial alarm
stimulus. His results and the available sensory physiology data were
used to develop a model of predator detection in flocks. Based on the
model, birds in flocks of various sizes were not taking the fullest
possible advantage of their potential collective detection ability.
The difference between potential and realized detection ability of the
flock may be explained as follows. The formation of groups increases
security for each individual in the flock, thus making it possible
for the prey to trade some of the security gained for other advantages.
This could be done by each individual keeping watch. The latter case
would free some members of the flock for alternative behaviors. Reduced
predation risk due to flock membership has been demonstrated to result
in a reapportionment of flock members time budgets (Murton, 1971;
Siegfried and Underhill, 1975; Inglis and Isaacson, 1978; Lazarus, 1978;

Diamond and Lazarus, 1974; Lack, 1968).

Powell (1974) found that Starlings share watchfulness while feeding in flocks, while Murton (1968) and Rassa (1977) noted that subordinate individuals do a disproportionate amount of watching, and thus exhibit a reduced feeding rate. These authors also noted a spatial context to the dominant-subordinate watchfulness relationship, with dominant birds located in the center of the flock. This idea is consistent with the observation that in colonial nesting birds, dominant individuals occupy the nest sites near the colony center where predation on nests is less than at the periphery (Coulson, 1966; Patterson, 1965).

The arguments developed so far lead to the conclusion that a flock of very large size would be maximally adaptive for detecting danger. However, in a large flock the flock members might physically occulde the visual field of neighbors, and thus negate the benefit of increased numbers of scanners for detecting a predator. In the case of a three-dimensional flock, only peripherally located inidividuals would be able to detect an approaching predator. If the shape of a typical globular cluster flock is approximated to a sphere (Heppner, 1974), the percentage of the total number of birds in the flock located at the surface changes predictably with flock size. The ratio of the surface area of a sphere to the volume decreases with increasingly larger spheres. Larger flocks would thus consist of a greater number of birds, but a smaller percentage of the total number would be located at the surface of the flock. Increasing the size of a cluster flight formation past some critical number of birds would not result in an increase in potential for the flock to detect and react to a predator. Rather, there would be a decrease in the relative number of effective

"watchers" in the flock, and signals from "watchers" would have to travel greater distances and to a larger number of neighbors in order for the warning function of flocks to be effective.

Another problem of large flocks concerns the disrupting effect of a potentially large number of false alarms (Treisman, 1975). The increase in the number of birds in a flock would result in a greater probability that at least one member of the flock would initiate a group reaction by giving a false alarm, or by inappropriate response to a neighbor. Davis (1975) studied this problem and showed that the type of response demonstrated by individuals in flocks may be a function of flock size. He noted that the response elicited by disturbances varied systematically with the size of the flock. As flock size increased, the responses changed from taking wing, to flight intention movements, to orienting responses. This safeguard mechanism may reduce the problem of large flocks being continually perturbed and distracted.

Superior ability in detecting predators is only one potential advantage of flocking behavior. Flock members may derive protection from predators by the juxtaposition of neighbor's bodies between themselves and the predator. Williams (1964) first suggested that schooling behavior arose from a kind of defensive hiding in which a threatened fish placed itself among other fish. In doing this a fish could both reduce its conspicuousness, and place other fish between itself and the predator. Hamilton (1971) considered that an animal with near neighbors would have a smaller domain of danger. Thus, the selfish advantage to those individuals who sought cover by staying close to their neighbors might result in a tendency to aggregate. He considered

it obvious that predation on individuals outside a flock would select for centripetal behavior.

Pulliam (1973) pointed out that since 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. Treisman (1975) argued that this would tend to result in the disband-ment of the flock, an argument which neglects the fact that there may exist a distinct disadvantage to the first individuals to disband from a flock. The disadvantage could be twofold. Flocks are thought to offer passive structural protection from attack (Mohr, 1960; Tinbersen, 1951; Eibl-Eibesfeldt, 1962; Charnov, 1975). Individuals leaving the flock would lose this advantage. Birds leaving the flock would also become the odd prey item in the vicinity of the predator, exposing themselves to increased hazard from predators (Mueller, 1975).

Howland (1974) discussed the relative importance of speed and maneuverability to optimal strategies for predator avoidance. He suggested that zig-zagging evasive maneuvers are important to the prey, and that the timing of each individual in staying with the group is very important. Individuals that do not move with the flock are behaving differently, and in theory will selectively be pressed upon. This concept is expanded in Eshel's (1978) hypothesis concerning the processes operating within groups of evasive prey. He suggested that dominant individuals may lead the group in an evasive path designed to provide themselves with structural protection and to expose the less fit individuals.

Dominant birds could gain an advantage by being located within the center of the flock structure, or in areas optimal for predator avoidance during an attack. If the positions of birds within airborne cluster flocks remain relatively fixed, a bird in the center of the flock may receive the most consistent benefit. A position on the surface of the flock could result in either minimum or maximum structural protection, depending upon the direction from which an attack occurred. The direction from which an attack occurred would also have an effect on the ability of birds to detect and respond to an attack. A position on the surface of the flock could result in a bird being the first to detect a predator, or the last bird to receive an alarm signal which travelled through the flock. Peripheral positions in a flock result in highly variable benefit both in potential for structural protection, and in timely response to predators.

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 to the response of many flocks to a predator (Nichols, 1931; Tinbersen, 1951; Mohr, 1960; Dill and Major, 1978). The effectiveness of a fixed position versus a variable position strategy depends upon the extent to which birds can move about within a turning and wheeling cluster flight formation. The question of mobility of birds within a flight formation has not been addressed, most probably because there exist no studies which have attempted to track the positions of individuals within an airborne flock.

Symons (1971) has pointed out that almost all studies of fish schooling behavior have depended either directly or indirectly on the accurate measurement of inter-individual distances within the schools. The photographic techniques used in three-dimensional analyses of fish schools are carried out in the laboratory where boundary conditions are controllable. Bird flocks require an enormous space for the execution of turning and wheeling maneuvers. The technical problems associated with field studies of flock geometry have been prohibitive to the point where there exist fewer than six studies relating to airborne flocks, with only one study attempting three-dimensional analyses. As a result there is no information currently available to describe fully the activities of birds flying in flocks.

Heppner (1974) summarized the principal characteristics of true flocks. He noted that the activities of flock-members tend to be synchronized such that birds head in the same direction and maintain even spacing. Heppner also differentiated between organized flocks in which birds fly in single file or columns (linear flocks), and flocks which have a three-dimensional structure (cluster flocks). Birds which fly in the cluster configuration include Starlings, many shore-birds, and Pigeons. This study presents the behavior of birds flying in cluster flocks.

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; Nachtisall, 1970; Gould and Heppner, 1974).

Dill and Major (1977) made the first analysis of the internal three-dimensional structure of Starling and Dunlin flocks. Their technique involved single, stereo-photographic samples of many different flocks of the two species of birds. Data were analyzed to determine statistically the flock geometry of the two species. Although useful for establishing the internal structure of an airborne flock for any one instance in time, their method is not applicable to investigations of flock dynamics.

The computerized, photographic analysis technique introduced here was developed specifically to provide the first quantitative description of the turning process in cluster flocks. I monitored the three-dimensional structure of flocks over time, and documented the changes in internal geometry of the flocks. The flight paths of each bird in the airborne flock were tracked so that the behaviors of individuals which resulted in observed changes in flock geometry could be readily identified.

Previous studies have filmed birds in straight and level flight. Such flocks are in the polarized state of group organization (Shaw, 1978), in which individuals in the group face in the same direction, proceed at the same rate of speed, and maintain precise position relative to each other. Birds in the flocks I monitored maintained a compact flock structure, but may not have been in the polarized state.

Breder (1976) presented a detailed model of the optimum geometric relationships between individuals in schools or flocks in the polarized 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, 1965; van Olst
and Hunter, 1970). Each individual, and a spherical shell of space
around it, is thus considered as a unit sphere. Flocing or
schooling can therefore be considered as a packing together of these
spheres. Various three-dimensional lattices, and the maximum packing
of unit spheres therein are described.

Functionally, the model 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 approximate a diamond shape (Weins, 1973). Three-
dimensional analyses of the distribution of fish in schools have demon-
strated this type of deployment (Cullen et al., 1965; Hunter, 1966;
Pitcher, 1973). The applicability of the model to globular flight
formation is shown in Dill and Major's (1978) nearest neighbor
analysis of Starling and Dunlin flocks.

An interesting aspect of the above model is the restriction on 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 precise geometric pattern, certain
areas of the flock or school represent forbidden paths of direction
of travel. These forbidden sectors 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. Functionally stated, a group must expand to make a sharp
turn, and as the group compacts 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 once the structure started to become compact, and 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. The present study asked how, or if, the restrictions stated in the model dictate the adaptive strategies that are available to birds within cluster flight formations.

The final aspect of my study focused on the relationship between dominance rank of individual birds and their position in the airborne flocks. I monitored the positions of birds of known dominance rank in order to investigate whether dominant or subordinate individuals were deployed in specific areas within the flocks, or if individuals of specific dominance rank are deployed near individuals of similar or dissimilar rank.

MATERIALS AND METHODS

A photographic record of the flight flocking behavior of Birmingham Roller pigeons was made over a five week period during the summer of 1980. The flock of 12 birds used in the study was housed in a loft located adjacent a large turf farm. The use of a flock of trained pigeons for filming and analysis provided several advantages. Birmingham Roller pigeons fly in cohesive cluster flight formations. They are large birds, each unique in color and marking pattern, and were thus well suited for any type of photographic analysis (see Appendix A). The time and location of flocking behavior could be controlled. The control of when birds were released from the loft allowed for minimizing the effects of meteorological conditions on flocking behavior. Filming was done on clear days when wind speeds did not exceed 18 Km/hr.

Although all 21 birds were released 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 the loft for approximately one hour. Birds not flying with the flock perched on the roof of the loft and could be easily identified. Identification of individual birds within the airborne flocks was possible.

Simultaneously exposed negatives were taken 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 motor drives were connected to a common electrical control unit so that both cameras fired simultaneously (single frame rate).

The deployment of the cameras was orthogonal. The cameras were mounted on tripods, raised to the same elevation, and aligned such that the interaction of their optical axes formed an angle of 90°. When viewed from above, the cameras would be located on opposite ends of a diagonal bisecting a square of dimension 60.8 m per side. Both cameras pointed at a common third corner of the box. The resulting area of overlap of the visual fields of view of the cameras approximated a 1000 m^2 square. The cameras were activated from a remote position when the investigator determined that the flock was within the field of overlap.

Photographic samples of the flocks were taken at 650 (+2)msec 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 which synchronized the motor drives lit each time the still cameras were activated. The bulb was in the field of view of the movie camera, making it possible to mark the frames of movie film when the still cameras fired. The movie camera ran at a rate of 24 frames per second, resulting in a sequence of 16 frames of movie film (Kodachrome 25) between each consecutive pair of still camera photographs. The more finely grained information obtained from the movie film was helpful in tracking the paths of specific birds within the flock.

Kodak Panatomic-X film was used in the still cameras. Film was exposed at F1.8 (1/1000) and developed according to manufacturer's

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

As the exact magnification involved in making each print was used in the analytical procedure for calculating the positions of birds, a non-standard 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 mm ($\pm$0.05 mm). Measurement of the image of the sprocket hole on prints proved the most convenient method of determining the enlargement involved in making the prints.

Image analysis was done by mounting the prints on a light table and measuring each bird's position on the print with digital readout calipers (Brown & Sharpe DigiCal). 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. Cross referencing of photographs taken from the two perspectives aided in such approximations.

ABSOLUTE POSITION: Information derived from the 8 X 10 prints was first used to establish where in three-dimensional space each bird

in the flock was located at each of the points in time at which photo-
graphic samples were taken. A Cartesian coordinate system was de-
fined for this point in space analysis. The X and Y axes of the
system were perpendicular, and crossed at the point of intersection
of the optical axes of the two 35 mm cameras. The plane of the X-Y
axis was level with the ground. The Z, or vertical, axis of the
system was defined as perpendicular to the X-Y plane. The elevation
(Z axis), and that bird's displacement along the horizontal grid
system (X-Y 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.

An example of the theory used to develop the computer programs
for position calculations is shown graphically in Figure 1. The
horizontal and vertical deviations of the image of a bird on a
negative from the center of that negative are the base of all calcu-
lations.

Data on the position of a bird on the negative from camera A
will locate that bird along a line orig-nating and extending from
point T (the optical center of the lens) to point B at infinity. The
bird could be anywhere along line TB. The trajectory of line TB
from point T is determined as follows.

The horizontal displacement (distance D_1) of the image of the
bird's head from the center of the negative (point R) is measured
to yield the length of side QR in triangle QTR. Side RT of the
triangle is the focal length of the camera lens when focused at

infinity (58 mm). Angle B in triangle QRT can be expressed as tan(QR/RT). Triangle QRT and MET are corresponding right triangles so 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 TB on the Y axis.

The vertical displacement of the bird's image from the center of the negative (distance D_1) is measured to yield side QA of triangle QAT. Side QT can be determined from the previous step in the analysis. Triangle QAT and TFE are corresponding right triangles. The elevation of line TB in the vertical plane (angle 0) can thus be determined in a manner similar to that used to find the horizontal displacement of line TB from the X axis.

The same processes were used on data from camera B to locate that bird along line CD. The intersection of lines TB and CD defines point F, the position of the bird in three-dimensional space.

The process of establishing the X, Y, and Z coordinates of point F varied depending on the position of the bird relative to the optical axes of the cameras. In the present example the bird is located in quadrant II of the horizontal plane. The bird's position at point F is directly above point E on the X-Y plane. Triangle TFC links the bird with the focal points of the two cameras. Distance TC of triangle TFC is the distance between the cameras (68 m). Measurement of distance D_1 on the negative of camera A yields angle B_1 (B_1 = inverse tan(D/58)). Angle T of TFC can then be expressed as B_1 + 45. Measurement of the horizontal displacement of the image of the same bird on the negative of camera B yields the angular deviation in the horizontal

plane of line CF from the Y axis. This value is subtracted from $45°$ to obtain angle C of triangle TFC. Angle F of this triangle is easily calculated as 180 minus the sum of angle T and C. All internal angles and side TC of triangle TFC are now known. Side TF is then equal to TC*tan(angle C).

The elevation of point F above the horizontal plane can be calculated by determining the length of side EF in triangle TEF. Side TF and angle 0_1 of the triangle are known from previous calculations. Distance EF, the elevation of point F, can be expressed as tan(0)*TF. The remaining side of triangle TEF, side TE, is easily calculated as TE=cos(0)*TF.

The position of the bird along the Y axis (side ME of triangle MET) is given by TE*sin(B). The displacement of the bird along the X axis is determined as follows. The distance from the optical center of the camera lens to point S is constant (TS=68 m). Side TM of triangle MET can be calculated as TM=ME*tan(B). Distance TM must be subtracted from 68 m (f TM>68 m), or 68 m must be subtracted from distance TM (if TM<68 m), depending upon where point M lies on the X axis.

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

$$D = (X_R - X_N)^2 + (Y_R - Y_N)^2 + (Z_R - Z_N)^2$$

Subscripts R and N in the formula refer to the reference (R) and neighbor (N) bird. Each bird in the flock was analyzed in turn as the refernce bird for every point in time. 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 distances categories, and the associated mean values, were plotted over time to graphically represent 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 is thus a true 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.

RELATIVE POSITION: The real space positions of birds were used in a second step of the analysis which assigned positional relationship to birds in the flocks. The terms right, left, above, and below are a function of the flight direction of the flock. The difference between birds' absolute positions in three-dimensional space and their positions relative to each other with reference to the flight direction of the flock is illustrated in Figure 2.

The absolute positions of birds A and B on the Cartesian coordinate system is the same in Figures 2a and 2b. The birds are at the same

elevation above the X-Y plane. If the direction of travel of the birds corresponds to flight path 1 (Level flight in Fig. 2a) bird B is located directly behind bird A. If however, the direction of travel of the birds is as represented by flight path 2 (a dive in Fig. 2b), the position of birds A and B relative to each other is very different than that seen in Figure 2a. In the latter case bird A is in front of (distance Q) and above (distance T) bird B.

Changes in the positions of birds over time were used in the second step of computer analysis to continually determine 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 mean flight path of the flock were then determined using methods described by Batschelet (1965).

The original Cartesian coordinate system was shifted in several steps to obtain relative positions of birds within the flock (Fig. 3). The first shift of the axes adjusted for the horizontal component of the direction of travel of the flock. The X-Y plane was rotated on the Z axis so that a heading of zero degrees corresponded 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 the X-Y plane was included or declined to correspond with the vertical component of the flight path of the flock. The last step of adjustement involved placing the rotated axis sytem at the geometric center of the flock.

A rotated and adjusted system of axes was made for each but the first time period in the series of photographic samples. The positions of birds at time N+1 were recalculated in reference to a coordinate system defined by the flight path of the flock from time N to time N+1. The resulting series of plots of birds' relative positions on the X-Y (flock as viewed from above) and X-Z (flock was viewed from the side) planes yielded information on left, right, 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.

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 tendem 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 1/1000. The cameras were electrically activated from the common control unit at 500 msec intervals until the ends of the 36 exposure rolls of film were reached. Analysis of the exposed negatives indicated that the two cameras consi-tently fired at exactly the same time (+ msec), and the time period between firing remained 500 msec (+1.5 msec) for the entire 36 frames (Appendix B).

A field simulation was conducted to determine empirically the accuracy and precision of the photographic and digitizing methods employed in the study. A three-dimensional test "flock" in which the distances and angular relationships between "birds" were known 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 $\pm$ 2.6%. In addition, each of the series of photographic samples of the model flock provided essentially the same estimate of the true flock geometry (Appendix C).

DOMINANCE: A group observation method rather than staged, paired encounters was used to study dominance in the flock. The activities of the entire flock were observed in the loft and selected indicators of dominance recorded. Observations of interactions between birds in the flock were made on alternate days for the duration of the study. Each observation period lasted 90 minutes, with 45 minutes spent at each end of the loft. Two observation areas were used to minimize site-dependent dominance (Brown, 1975).

Agonistic encounters between birds and the act of supplanting were used to establish a win/loss matrix for each observation period. Three summary matrices, each representing six observation periods, were formulated and used to establish dominant and subordinate birds in each of the airborne flocks analyzed. As Pigeons do not form linear dominance hierarchies (Brown, 1965), data from the dominance matrices were used to investigate whether individuals of either extreme rank behaved differently than other birds in the flock.

RESULTS

The turning and wheeling maneuvers of flocks descending to low flight around their loft were photographed. Seven film trials representing a variety of flock flight behaviors were analyzed. All birds housed in the loft did not fly with the airborne flocks during. the filming of each trial. Each trial therefore varied in the relative composition of individuals and the total number of birds present in the flock.

Table 1 shows the composition of the flocks for each of the seven trials. Three types of information are given for each trial. Assigned numbers were trial specific labels used to distinguish birds in the series of photographs for a trial. Identification numbers were given to each bird and used throughout the duration of the study to identify specific individuals (Appendix A). All members of airborne flocks which could be identified have entries in Table I for the associated dominance rank of that individual.

A complete analysis will be presented for three trials representative of the different behaviors observed within the airborne flocks. The first trial presented (trial 7) demonstrates the types of information available from the study. Summary data for five trials are shown for flock speeds, compatness, and turning arc, as well as for distributions of distances to first, second, and third neighbors. Dominance data are summarized for all seven trials.

Table II shows the three-space Cartesian coordinate positions of the 11 birds in trial seven. This information is shown graphically in Figure 4. Figure 4a shows the positions, as seen from above, of all birds in the flock at each of the six instances in time at which

the flock was photographed. The horizontal spread of the flock at each point in time is readily seen. As the time period between photographic samples of the flocks remained constant at 650 msec, the relative distances traveled by birds between photographic samples of the flocks remained constant at 650 msec, the relative distances traveled by birds between points in time can also be seen. Figure 4b shows the elevation of the geometric center of the flock at each of the six time periods. Inspection of Figure 4 shows that the flock was executing a right turn of approximately 90°, was losing altitude and was possibly accelerating.

Nearest neighbor pairings and associated separation distances, as well as distances to all neighbors of each bird, were calcualted for the six time periods (Appendix D). The average distance to first nearest neighbor, and the mean separation distance between flock members are plotted for each time period in Figure 5. Mean separation distance reflects distance between all combinations of individuals in a group and is thus a good measure of the compactness of the group (Hunter, 1966). Figure 5 shows that the flock became more compact from time one to time two, and then expanded. If both parameters in Figure 5 changed over time such that the curves were parallel, the information derived from the plot would indicate only that one flock was expanding or compacting. For example, from time two to time four to time five the flock structure continued to expand, while at the same time average distance to first nearest neighbor decreased. This combination of changes in the two parameters is an indication of the formation of nearest neighbor pairs or subgroups within the expanding

flock.

More complete information on flock structure at each point in time of trial seven may be obtained from plots of all neighbor distances within the flock. Interpretation of neighbor distance plots with reference to: (1) the height and slope of the line connecting mean neighbor distance, (2) step versus smooth linear increase in distance to neighbors, and (3) distribution of distance values within the neighbor classes, can be used to establish flock structure.

Neighbor distance plots for each point in time of trial seven are shown in Figure 6. Figure 6a shows the distributions and associated mean values for distances to increasingly remote neighbors within the flock at the first time period at which the flock was photographed. There is a near linear increase in nearest neighbor distances (R^2 = 0.78), indicating no subgroups of clumps. The distribution of values within each neighbor class suggest that no stragglers existed at this time.

Figure 5 indicates that the flock compacted from time one to time two, and then expanded. Figure 6 allows a quick description of how the flock expanded. The dotted lines in Figures 6b through 6f are a trace of the solid line connecting the mean neighbor distances at times one. This dotted line appears as a reference so that changes in the distribution of neighbors can be more readily seen.

The changes over time in the line connecting mean distance to neighbors could take several forms representing either an expanding or compacting 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 which was parallel to the solid line of time one, but representative of difference 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.

Figure 6b shows that the flock became more compact from time one to time two due to a decrease in distances to all neighbors. The occurrence of high values in the distributions for third through tenth neighbor in Figure 6c indicates a group of three birds broke away from the main body of the flock. The only distribution of birds in a flock which dould result in the plot of Figure 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 so that their distances to third through tenth neighbors appear as the high values in the classes. Figure 6d shows that the flock had become dispersed at time four, with no clear indication of stragglers or clumps.

The clumped distribution of the birds indicated at time five in Figure 5 is confirmed in Figure 6e. A Scheffe multiple comparison test of the distance distribution of values to nearest neighbors was performed to check if the linear relationship at time one had become stepped at time five. The test confirmed that the line connecting mean values of nearest neighbor distances has two distinct segments. The first segment describes the distributions of neighbors one through five, and the other segment describes the distribution of neighbors six through ten (F=3.22, df=9.90, P<0.05). This

Those birds, such as individuals six, two, and eleven, whose flight
paths were the same, maintained positions close to each other over
time. Birds five and eight flew together on a flight path which
described a different arc than that of birds two, six and eleven.
The redistribution of birds within the flock as seen in Figure 7 is
thus due to the fact that different birds, or groups of birds, had
flight paths whose arcs were either of different radius, or of
similar radius but which originated at different centers. The latter
situation would result in arcs which crossed, and in the rotation of
relative positions of birds.

Birds which continued to fly on a course such that they maintained
positions close to each other will be said to be part of a closely-
flying subgroup 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 two, six, and eleven as a CFS during the six time
periods in trial seven, it is of interest that the previous graph
analyses which established clumped distributions of birds within the
flock indicated these three birds as a physical clump only at time
periods two and five.

Figure 8 gives a quantitative confirmation of the shuffling of
birds' positions within the flock. For each of the five points in
time of trial seven at which relative positions could be determined,
the birds were ranked in order of distance from the front of the
flock. A Spearman rank order correlation could then be used to

indicate the degree of association between the front-to-back sequence of birds at any two sequential periods in time. Four correlations were calculated to indicate the measure of assocaition between all rankings involving a time gap of one (sequential ranking tested). High correlations for all tests involving a gap of one time period would indicate short-term stability. I was also interested in the association between rankings made at the beginning and end of the trial. If the positions of birds within the flock remained constant over time, the correlation between front to back ranking of birds involving two sequential time periods would be the same as the correlation between the first and last time periods. A series of correlations between front to back rankings of birds was made, controlling for an increasingly longer time interval between the two periods at which the rankings were established. Figure 8 shows a decrease in the association between front to back sequence of birds with increasing time sap between sample periods, indicating that the internal flock structure was not stable over time.

TRIAL 8: Trial eight consisted of eight photographic samples of a flock of 16 birds. The flock executed a roller-coaster type turn. Figure 9 indicates that there was a slowing down and climbing during the middle portion of the turn. The latter stages of the turn were characterized by an acceleration and diving of the flock.

Flock compactness and distance to first nearest neighbor at the eight periods in time of trial eight are shown in Figure 10. The flock became more compact during the beginning of the turn, dispersed during the middle of the turn (time 5), and then became

compact.

The distributions of distances to all neighbors are seen in
Figure 11. The initial compacting of the flock was due to a
residtribution of birds so there was a decrease in distances to
more remote neighbors. At times four and five there was an
increase in distance to nearer neighbors, indicating a breakup of
the flock structure. A large decrease in distances to all neighbors
occurred by time six. The close neighbor distances indicative of
a compact flock were maintained throughout the rest of the trial.
A single straggler was seen at times five and six.

Figure 12 shows the flock as viewed from above, and from the
side at seven of the time periods for trial eight. The overall
shape of the flock changed from a front echelon with little vertical
spread (time 2), to a sphere. Changes in the relative positions of
individuals were evident. The positions of many birds rotated around
the Z axis in a counter-clockwise direction over the period of time
during the flock was photographed.

The repositioning of birds within the flock over time is shown
in Figure 13. Correlations between front to back rankings of birds
decreased with increasing time gap between the periods at which birds
were ranked. Although the flock was not stable in terms of constant
relative positions of flock members, the shifting of positions
within the flock did not result in an expanding flock structure.

TRIAL 2: Trial two shows a flock of dispersed individuals and sub-
groups which merged to form a single, core group. Figure 14 shows
the flock of 14 birds viewed from above at six instants in time.

The flock turned approximately 90° to the right, while maintaining level flight. Figure 15 shows that the flock expanded slightly, and then continued to become more compact over time. Distance to first nearest neighbor decreased from time one to time two, while during the same time overall flock structure loosened. This indicates clumps or nearest neighbor pairs at time two.

Nearest neighbor distance increased from time two to time three, while flock structure became more compact, indicating that the nearest neighbor pairs of time two separated to form a dispersed flock. Mean separation distance and distance to nearest neighbor decreased over the next three time periods.

The distributions of distances to all neighbors are shown in Figure 16. The high values in all the distributions of distance to neighbor indicate one bird was separated from the flock. The large difference in values of first versus second neighbor distance suggest that nearest neighbor pairs may have existed at time two. Figure 16c shows that at time three the line connecting the mean values of the distributions had separated into two segments, one describing the distributions of first through fifth neighbor distances and the other discribing distance values for sixth through eleventh neighbors. A Scheffe multiple comparison test of the distributions confirmed that the line connecting mean values consists of two segments ($F=2.4$, $df=12.143$, $P<0.05$). Step increases in distances to neighbors, a situation suggesting the existence of clumped distribution of birds, exist at times three and four. The step distribution is not seen at

times five or six, indicating that the subgroups have merged into a single, core flock. Note the decrease in distance to all neighbors at times five and six, which also suggests the merging of subgroups to form a single flock.

The processes described above are apparent in Figure 17. Nearest neighbor pairs do exist at time two. Figure 17 (frame 2) shows neighbor pairs 6 and 3, 4 and 5, and pair 8 and 7. All birds except 2 and 14 have a close nearest neighbor. Groups 1, 9, 10, 11, 2 and 3, 4, 5, 7, 8 at time three, and groups 1, 9, 10, 12 and 3, 4, 7, 8 at times four, merged into a single flock by time five. Bird 14 was the single straggler at time six. The relative positions of birds changed over time. The shifting of positions is seen in Figure 18 as a decrease in correlation between front to back rankings of birds as the time period between rankings increases.

SUMMARY DATA: Summary data relating to sharpness of turn, flight speed, and elevation changes of flocks are given for each trial in Figure 19. These data were used to establish which parameters influence the flight speed of a turning flock. Figure 19a shows that birds in trial two executed a 95° turn. The turn was made while the flock was in level flight and maintaining a flight speed of approximately 21 Km/hr. There was no relationship between sharpness of a segment of the turn and flight speed maintained during that segment. Figure 19b shows that birds in trial six made a 180° turn while maintaining a slightly slower speed than the flock in trial two. Two of the sharpest turn segments in the horizontal plane were associated with the highest flight speeds. The flock in trial eight (Figure 19c) also made a

180° turn, and slowed down in the middle of the turn. The flight speed of the flock may have been influenced by the vertical rather than the horizontal component of the flight path. The flock was climbing during the period of time in which flight speed dropped. During the second half of the turn the flock started to dive and accelerate. The fastest speed attained by the flock was during this period of drop in altitude, a time also including the sharpest horizontal components of the turn. This trend is also seen in trial seven (Figure 19d) in which the flock accelerated and dove as it negotiated a sharp turn. The flock in trial nine (Figure 19e) accelerated as it dove, making the sharpest horizontal component of its turn while travelling the fastest. The data in Figure 19 indicate that the vertical component of a turn may be most influential in determining flock speed.

To faciliate comparisons between flocks in this study, frequency distributions of first, second, and third nearest neighbors for each trial were assembled (Figure 20). Note the difference in shape of the distribution between the loosely organized flock in trial six (Figure 20b) and the consistently compact flock in trial eight (Figure 20d). There is a tendency for flocks which changed in degree of compactness over time to have second and third neighbor distances distributed more normally than a consistently compact flock. The former trend can be seen in trials seven and nine. The latter trend is seen in trial eight, in which the distributions of second and third neighbors are skewed to the left.

DOMINANCE: Data collected during each trial were analyzed to establish whether dominance rank had an effect on behavior or position of birds within the airborne flocks. The observation sessions showing inter-actions between individuals in the flock are summarized in three dominance matrices (Appendix F). Each matrix consists of data from six 90 minute observation sessions. The matrices were used to establish a dominance rank order of birds for each of the three time periods during which filming took place. The ratio of the number of wins to the number of losses that each bird had as a result of its interactions with other flock members was used to establish the two most dominant and two most subordinate birds in each of the airborne flocks. Tests for an effect of dominant or subordinate status on position within the flocks thus involved only birds at either end of the dominance rank order. The mean distance from the center of the flock for all time periods in all trials was not different for the dominant group and the subordinate group (t=1.71, df=174, P>0.05), or from the average distance to nearest neighbor for the entire flock (t=1.18, df=519, P>0.05).

A final analysis utilized the rank order of birds established in the matrices to determine whether birds of high or low rank tended to associate with birds of similar or different rank. Figure 21 is a plot showing the summary pattern of association of dominance rank between nearest neighbors in the airborne flocks. The plot indicates a trend for association of birds of dissimilar rank.

DISCUSSION

A type of compact cluster flock commonly observed is the spherical ball reaction of some species of birds to predators (Mohr, 1960; Tinbersen, 1951; Dill and Major, 1977). The flight behavior of Birmingham Roller Pigeons is characterized by a continuously compact flock during the performance of turning and wheeling maneuvers. The first training flock of pigeons in my study was attacked by a Cooper's hawk on several occasions prior to the beginning of filming. The pigeons responded by performing evasive maneuvers while maintaining a compact cluster structure. Several birds which did not stay with the flock were selectively preyed upon. To discuss the present study in relation to adaptive strategies in airborne flocks I needed to first determine if I was really observing compact cluster flight formations. If this could be established, it would then be useful to document how the movement of individuals within the flocks either conformed to or differed from predictions of models which describe the deployment and movement of birds within three-dimensional flocks.

The mean distance to first nearest neighbor for the flocks in this study (153.8 cm) is similar to those reported by Dill and Major (1978) for Dunlin (70.0 cm) and Starling (145.0 cm) flocks. Absolute

distances to nearest neighbor as a measure of the density or compact-
ness of a flock is not sensitive to the size of the birds which are
spacing themselves apart in the flock. One can take into account
the size of the birds in a flock by computing the ratio of distance
to first nearest neighbor to the average size of flock members. The
range of values for the ratio in the present study go from approxi-
mately 4:1 which is close to the 3.25:1 ratio of tightly packed Dunlin
flocks, to 8.5:1 which is slightly higher than the 71.:1 ratio
reported for Starling flocks (Dill and Major, 1978).

The distance distributions for first, second, and third neighbors
in the seven flocks of this study also resemble those reported by
Dill and Major (1977) for Starling and Dunlin flocks. These types
of distributions have been attributed to birds that fly in tight,
relatively closely spaced flocks.

The polarized Dunlin and Starling flocks exhibited the internal
geometric construct predicted by Breder's (1976) model of optimum
packing. This construct has been observed in virtually all fish
schools studied to date. The pigeon flocks of my 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 did in
many cases 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 indicates that there is much less internal or 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 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 body
length apart.

The greater amount of relative empty space in the cluster flocks
may be necessitated in part by the medium in which birds travel,
and their speed. The empty space made it possible for birds to be in
transit through the flock structure during the time the flock was
turning. High angular deviation in headings of fish in schools
indicated a decrease in compactness, and breakup of the structure to
allow fish to negotiate a turn. A peak value in angular deviation
in headings of birds in the flocks of this study did not necessarily
signify a breakup of the flock structure. The potential for birds
to travel through the flock resulted in many cases in a more compact
flock at times of highest angular deviation of headings.

An understanding of the simultaneous occurrence of great internal
change, and maintained overall cohesive structure is best obtained
through an analysis of the turning process in the cluster flocks.
The redistribution of birds within the flocks always involved the
apparent rotation of individuals' relative positions within the
flock always involved the apparent rotation of individuals' relative
positions within the flock structure. Analyses of the flight paths
of birds revealed that individuals were not flying parallel arcs as
would be expected with a column type turn. A column turn involves

a situation in which birds maintain the same relative positions throughout the turn. The individuals remain parallel to one another such that samples of the flock taken at any point in time would yield a similar geometric construct and deployment of individuals within the flock.

Turns in this study were all sharp and seemed to involve a breakdown in any structure which may have existed prior to the turns. 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 would have implication to studies of leadership strategies 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. An example of the resulting change in positions of birds within the flock over time is shown in Figure 22. The plot shows that the crossing of flight paths of birds results in the counter-clockwise rotation of their relative positions within the flock. Such a pattern of repositioning of birds within the flock was observed in all the flocks in my 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 was seen in trial seven, in which birds three and ten travelled different arcs that approached at time five.

There is probably less behavioral 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 stay together throughout the entire course of a turn. In all trials some groups of birds continued to maintain positions close to 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 trial seven could occur. Pairs or groups of birds within a flock which describe similar paths through space may be considered CFSs. In trial seven the CFSs were also distinct physical clumps because the flock was breaking apart. CFSs in a flock which is compact and not expanding may not appear as distinct physical units within the overall flock structure. This situation existed in trial two. A group of birds originally on the outside edge of the flock relative to the turn, cut short. Another subgroup did not seem to 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 these 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 the flock at no time separated 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 which respond to each other over time in adjusting their flight paths. The concept of individual response to specific neighbors

has 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. Gould and Heppner (1974)
suggested that the Vee formation of geese is such that neighbors are
in the center of the visual field of following birds. It is very
common for pairs or small groups of birds to break away from and
then rejoin cluster flocks, a situation which 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).

Two aspects of turning in cluster flocks have been discussed.
The first involves the potential for birds to change relative position
within an airborne flock. A spherical flock structure involving
relatively fixed positions of individuals would offer distinctively
different advantages to peripherally and centrally located birds.
My study indicates 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 phenomena
of relocation rather than maintaining a fixed position in the flock.
A bird would not necessarily have to peel off from the surface of the
flock (Pulliam, 1973) to become separated from the flock. An individual
located in the center area of a flock could easily become a straggler,
due to positional rotation of individuals in a turn.

The second aspect of turning relates to the cues to which birds respond in altering their flight paths. 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 Km/hr and making a sudden, sharp turn, a slight delay in response could result in a very different arc of turning and 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.

These two aspects of turning in cluster flocks may act to influence how the potential for flocks to offer passive structural protection (Mohr, 1960; Charnov, 1975) and the selection of odd prey by predators (Mueller, 1975) interact in dictating adaptive strategies within airborne flocks.

Eshel (1978) proposed a strategy in which passive structural protection, selection of odd prey, mobility of individuals, and dominance are all important factors within groups of evasive prey. The behavior of the escaping group is described as consisting of a series of interactions between the prey and the predator, and among the prey. Dominant individuals in the group gain an advantage as a result of the interactions by initiating maneuvers which eventually expose weaker individuals. The results of my study indicated that there was a tendency for birds of dissimilar rank to take positions close to each other while in the airborne flocks. The selection could have been on the part of dominant birds, subordinate birds, or

mutual attraction. One possible explanation for the association
is that dominant birds are maintaining positions near subordinate
individuals in order to 1) insure potential use of the subordinate
individuals as structural protection in the event of attack, or
2) be in a position where they could most effectively perform
evasive maneuvers which would result in a subordinate bird being
singled out from the flock structure.

The continual redistribution of birds within turning flocks has
bearing also 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
Shollenbeger, 1979; Higdon and Carrson, 1978; May, 1979). Models
which relate various three-dimensional flock structures to
increased aerodynamic lift to all members of the flock may not apply
to flocks when flock members are turning in a manner described in
this study. The aerodynamic models assumed maintained and specific
geometric construct within flocks. The observed crossing of flight
paths, and changes in flock compactness in this study indicate that
birds could not long remain in the updraft segments of winstip vortices
from leading birds.

The birds within the flocks of Dill and Major's (1978) study were
deployed in a manner which would result in an aerodynamic advantage
to flock members. It is interesting to note that the flocks filmed
in their study 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 conditions the adaptive strategies of flocking relate to each individual's ability to protect itself rather than aerodynamic advantages. Some of the benefits of each type of flock configuration and behavior are exclusive to one type of flock. It would seem very likely however, that birds can easily and rapidly switch from an aerodynamic flock formation to a flock configuration in which evaisive maneuvers, staying with the group, and structural protection from neighbors minimize the threat of predation. Probably the turning and wheeling flocks observed in my study represent only one of the types of flocking behavior exhibited by birds which normally fly in a cluster formation.

Several results from this study may have bearing on future investigations of three-dimensional flocks. Two potential problems exist with the present dominance study. The first concerns the fact that pigeons do not form linear dominance hierarchies (Brown, 1975) so that dominance rank may be useful for establishing two distinct classes of individuals at either end of the hierarchy, but not for linear analyses. The second problem is that of site dependent dominance (Brown, 1975). A dominance relationship established under certain circumstances or areas may not be absolute. The problem in this study was that a pigeon's dominance rank as observed at the loft may only apply in the loft. Dominance rank established in the loft may not carry over to interaction within the airborne flocks.

The difference between physical clumps and CFSs suggested by this study provides the following guideline for requirements of sampling. A single sample of a flock can establish the geometric construct that exists at a particular time, but is insensitive to CFSs in a flock. The movement and redistribution of birds within a turning flock render analyses based solely on detecting physical clumps, or analyses based on nearest neighbor data from a single sample of a flock, of questionable value for establishing the processes responsible for maintenance of flock stability and structure. The above type of nearest neighbor analyses may establish artitrary associtions such as temporary neighbor pairs resulting from birds whose flight paths approach or cross at a point in time. Spatial analyses for clumped versus uniform or random distribution of birds based on single samples of the flock may be insensitive to CFSs or truely functional relationships which exist within the flock.

An important aspect of this study is the establishment of a method for obtaining a quantitative description of the structural changes and reorganization in airborne flocks. The plots of first nearest neighbor and mean separation distance were effective in establishing general trends in the changes in flock geometry over time. The plots of distribution of distances to all neighbors for each period in time provided more specific information. For example, the plots allowed me to establish whether changes in flock compactness were due to uniform response of all birds in assuming closer or more distant positions from neighbors, to the formation or merging of subgroups, or to the existence of stragglers.

This study provided the method of analysis, and descriptions of flock geometry which suggest what types of strategies are available to birds flying within cluster flocks. The next logical step in analysis of three-dimensional flocks would be to use either this method or some type of structural analysis method to study responses of birds in cluster flocks to a trained hawk, and to quantify the responses of flock members.

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Figure 1. Calculation of the positions of birds
in three-dimensional space. The
image of the bird at point F forms
on the 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 calcula-
tions).

NEGATIVE OF CAMERA A

CAMERA B

Figure 2. Effect of flight path upon relative positions of birds within the flock structure. Fig. 2a shows a level flight path in which bird A is directly in front of bird B. Fig. 2b shows a flight path involving a dive. In this case bird A is in front of and above bird B.

flight path 2

flight path 1

HORIZON

CAMERA A

CAMERA B

CAMERA A

CAMERA B

18m

18m

18m

18m

X

Y

Z

X

Y

Z

A

B
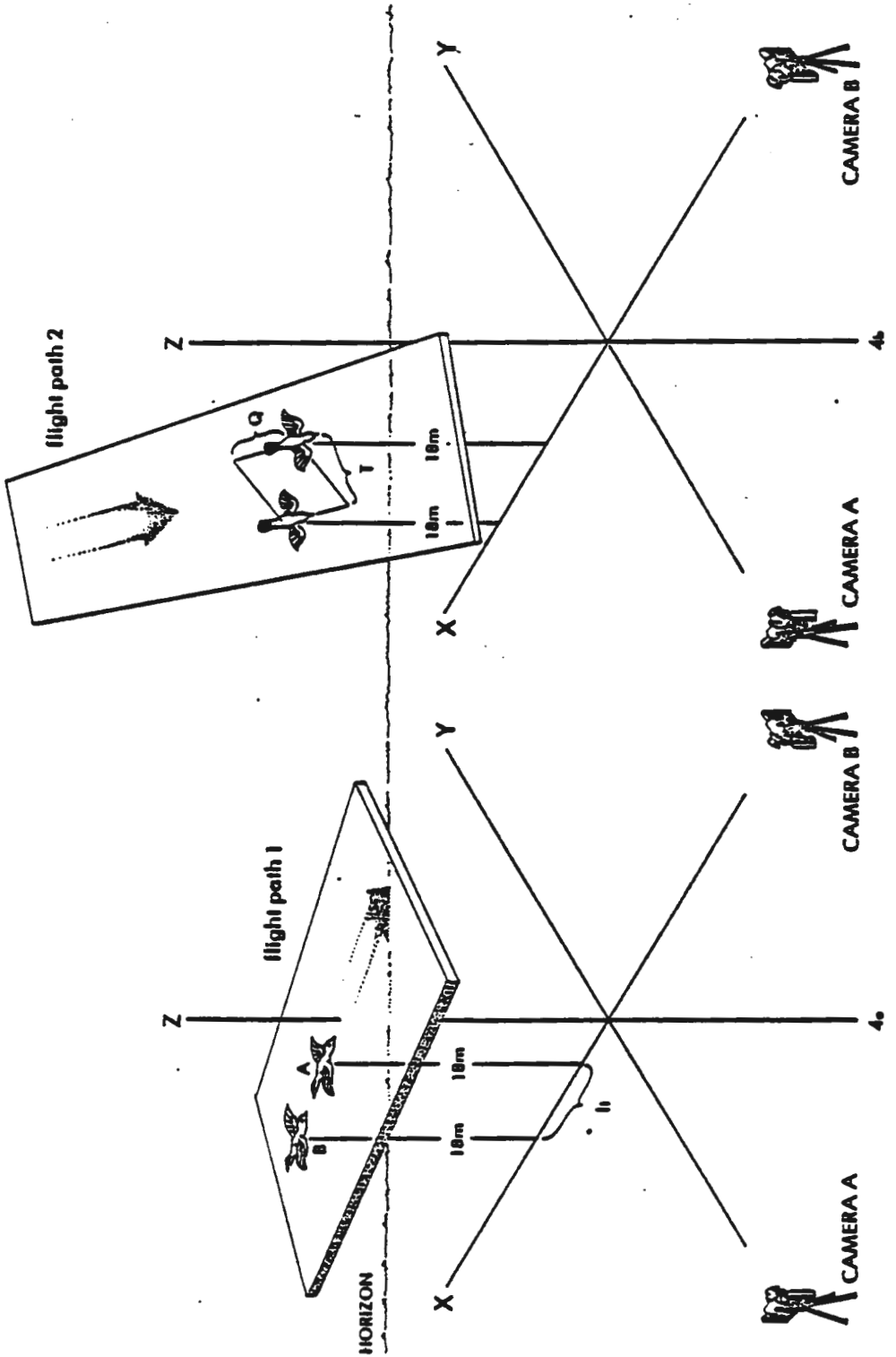
Figure 3. Calculation of the horizontal component
of the flight path of the flock.
Bird A as viewed from above at two
points in time is shown to have turned
to the right. Displacement along the
X-axis(ΔX), and the Y-axis(ΔY) is used
to determine angle θ, and thus the
flight vector of bird A. The sum of all
Xs and Ys were used to find angle
θ for the flock as a whole.
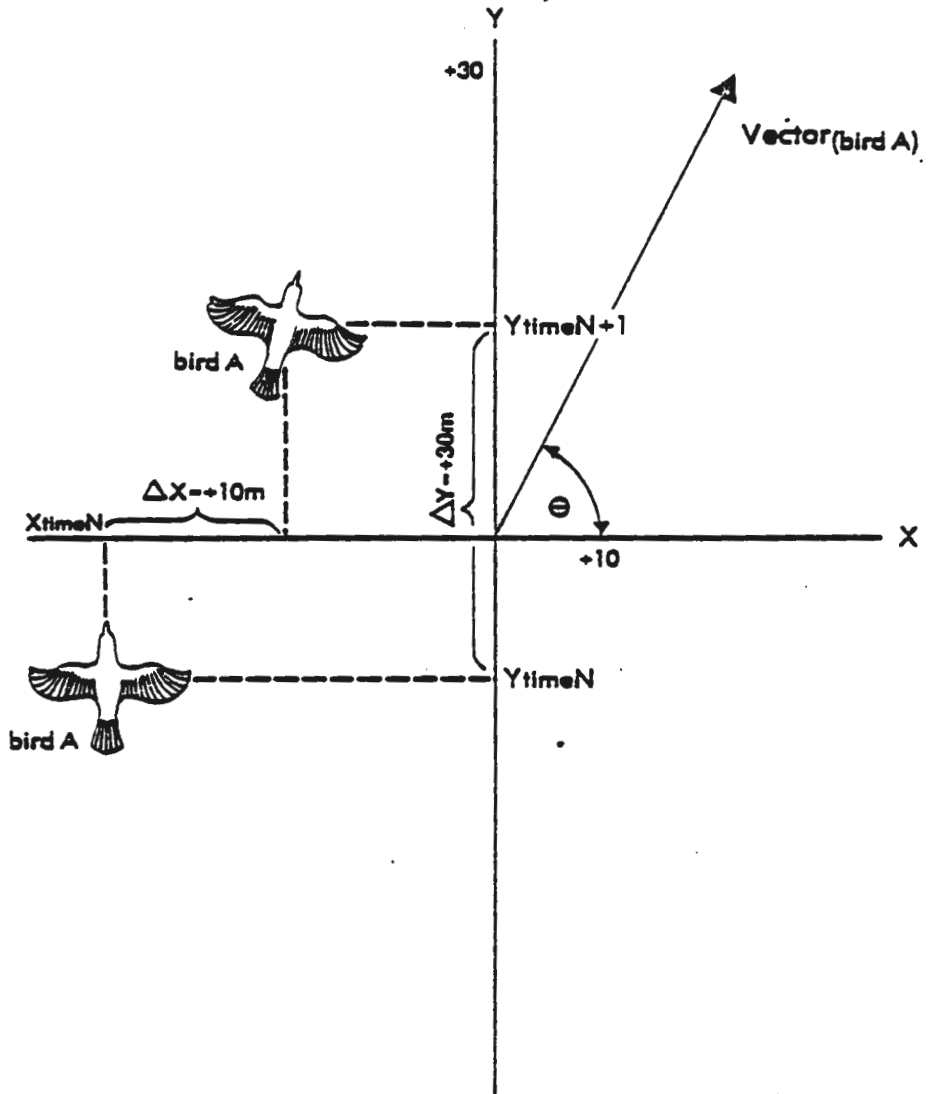
Figure 4.   Summary information on flock movements
over time. Figure 4a shows the flock
in trial seven as seen from above for
each point in time at which photographic
samples were taken. The deployment of
birds in the horizontal plane is readily
seen. Arrows indicate the mean direction
of travel of the flock. Figure 4b shows
the changes in elevation of the geometric
center of the flock. Note that the X-Y
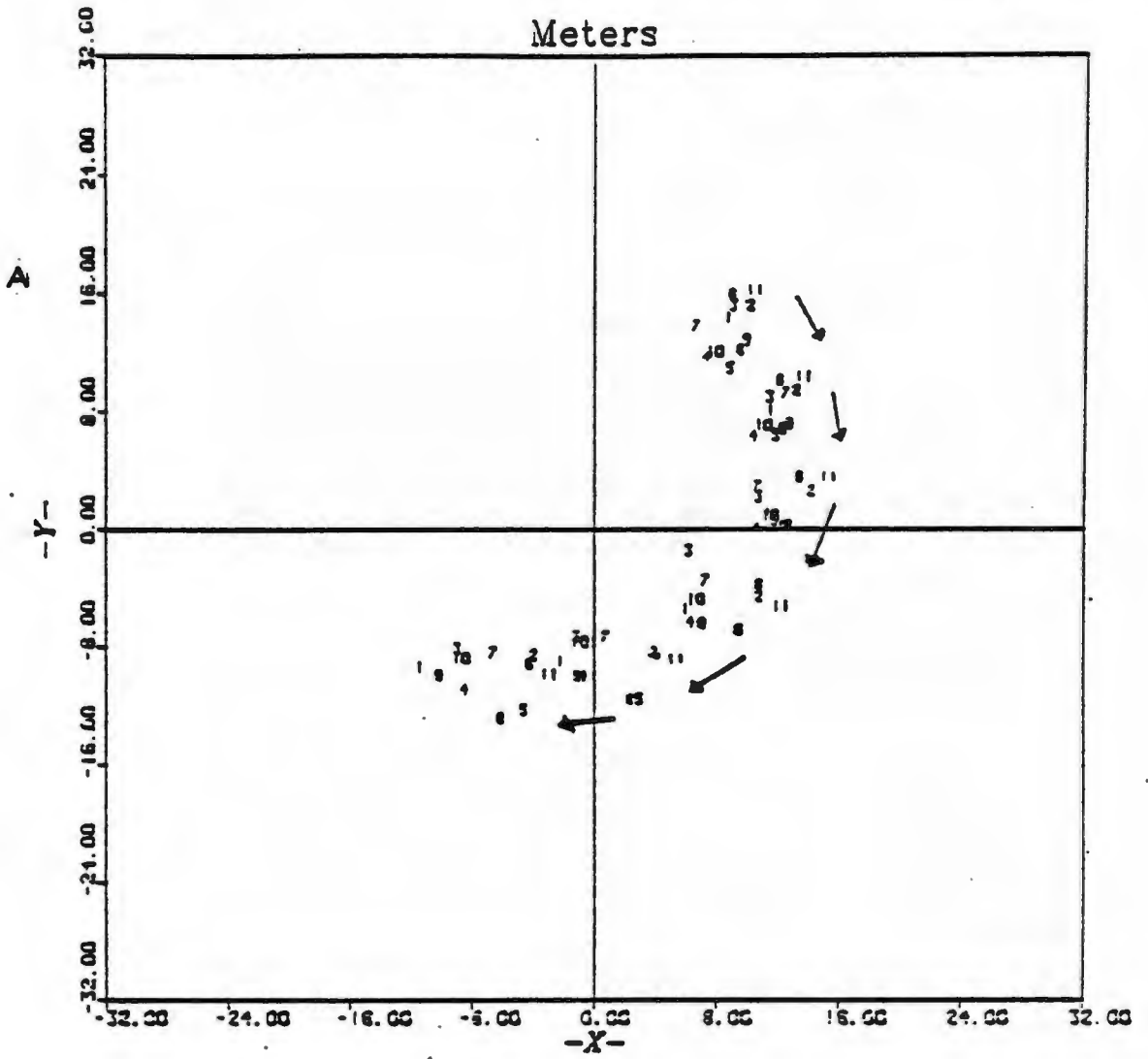plane was elevated approximately 150 cm
above ground level.

Meters

A

-Y-

-X-

B

ELEVATION IN METERS
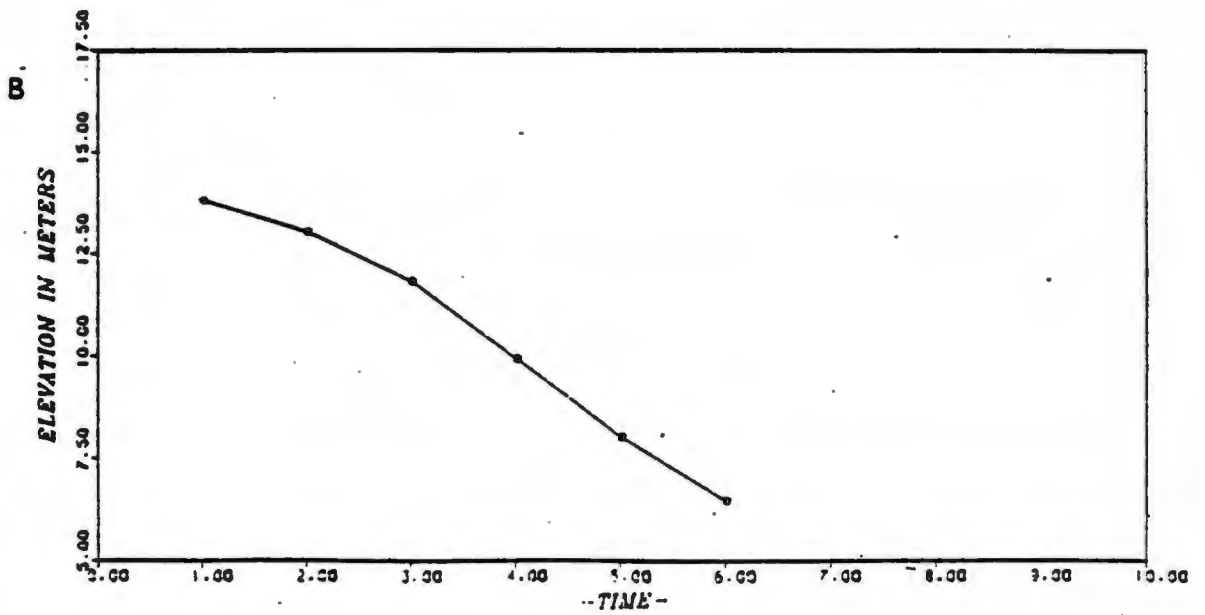
--TIME-

Figure 5.   Changes in values for mean separation
distance and mean distance to first
nearest neighbor for the six time
periods in trial seven. Various types
of combinations of change in the two
parameters are indicative of specific
types of deployment of flock members
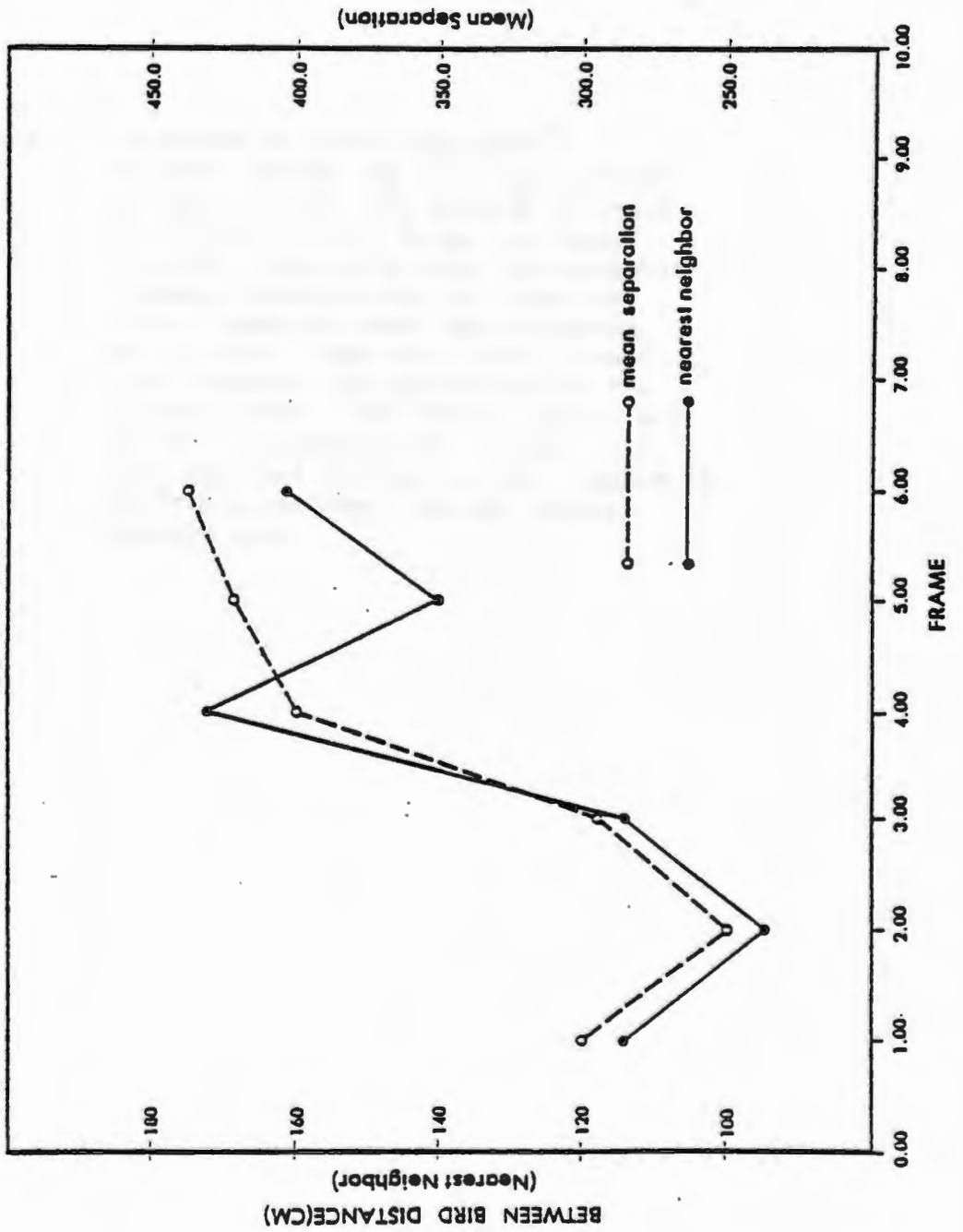(see text for full explanation).

Figure 6. Distances to first through N^{th}
neighbor within the flock are plotted
for each of the time periods at which
the flock in trial seven was photo-
graphed. Figure 6a shows the neighbor
distance distribution for time one,
while Figure 6f shows the distances
at time six. The solid line in each
plot connects the mean values of the
distributions. The dashed line in all
but the connecting mean values at
time one, and appears so that changes in
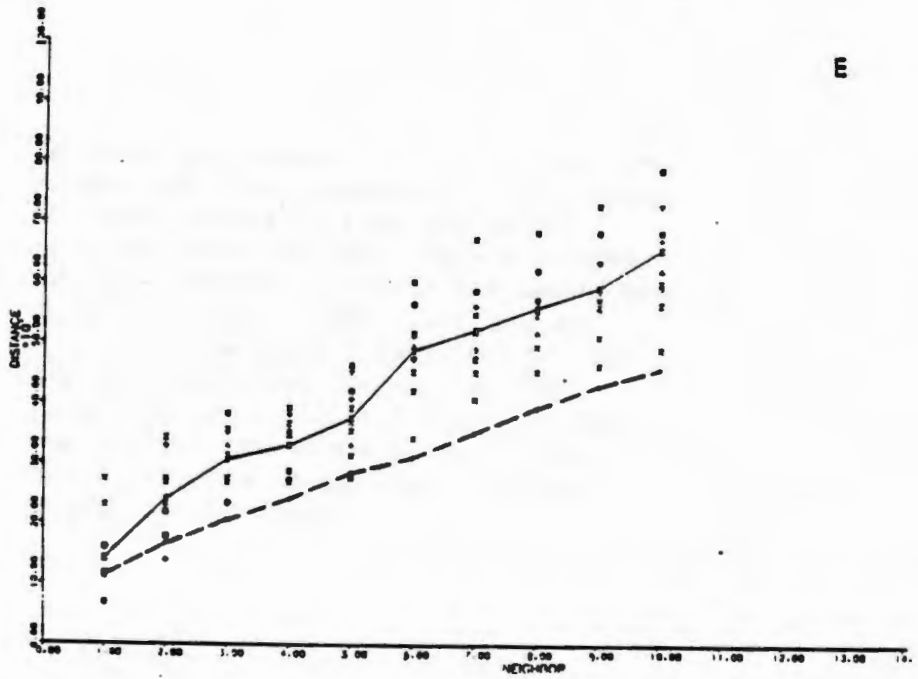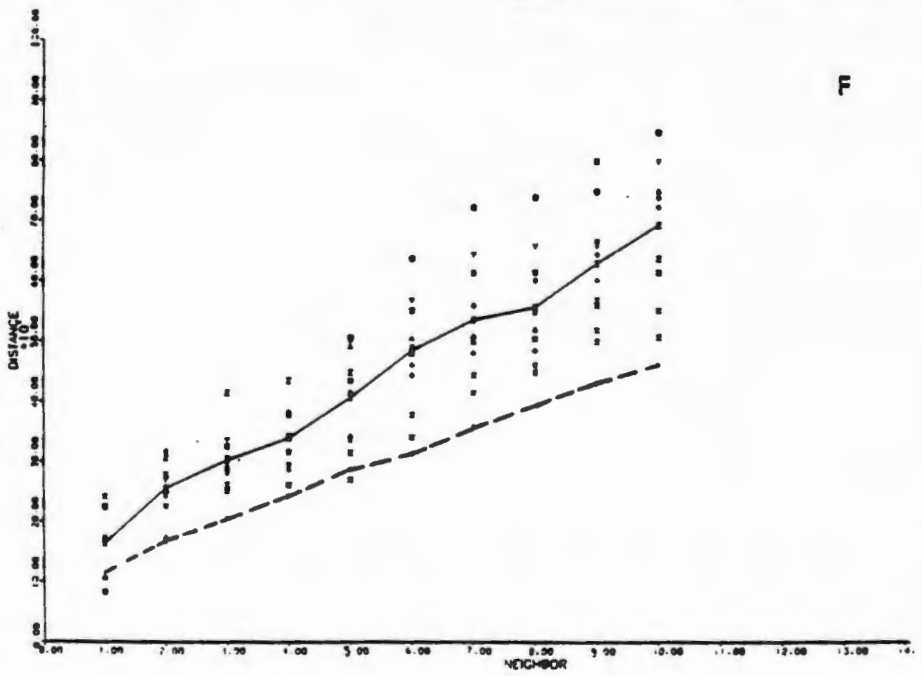distributions over time may be more
readily seen.
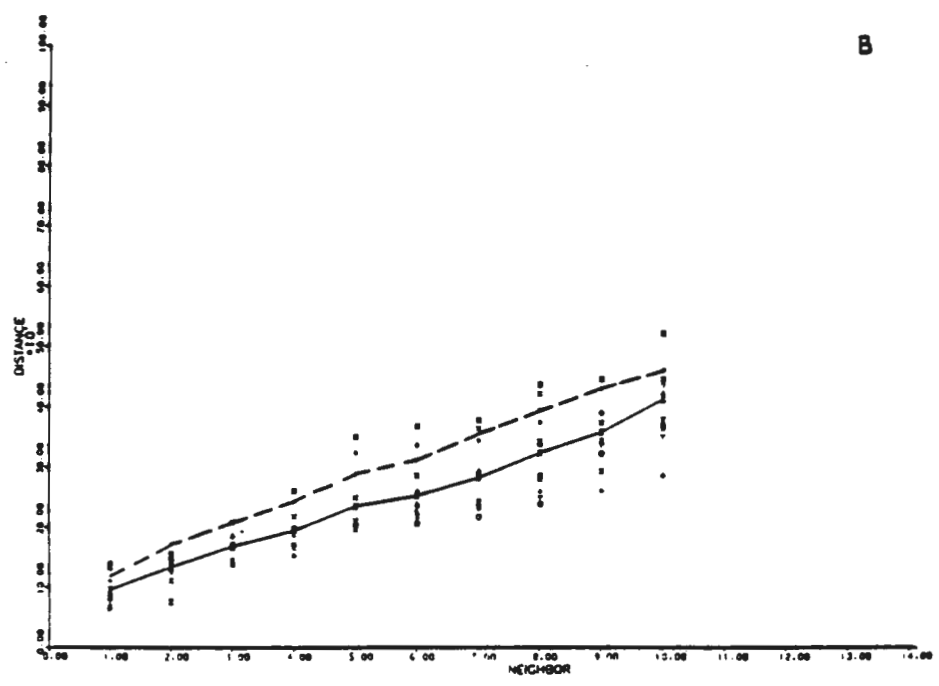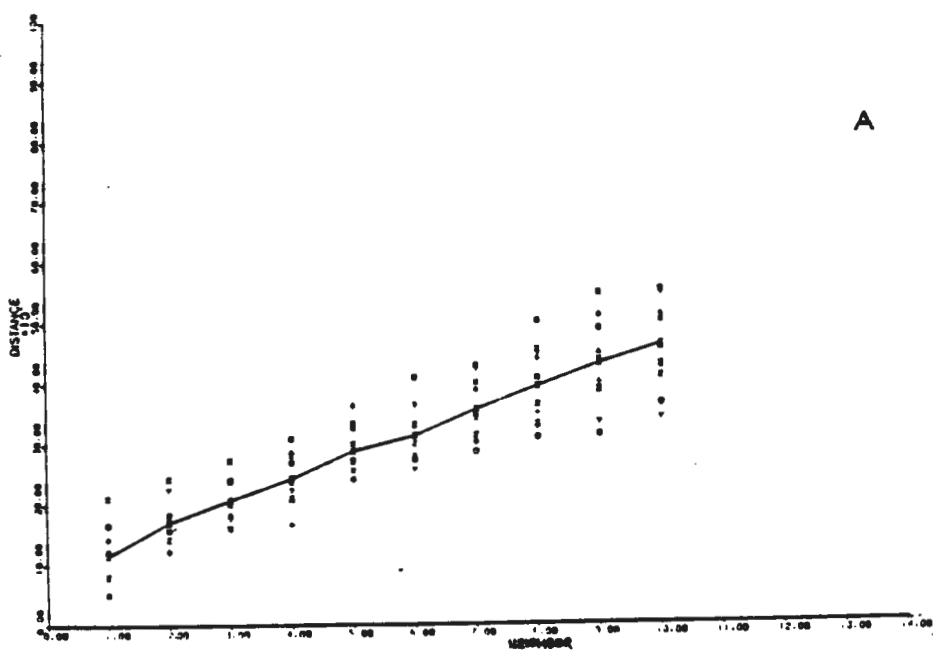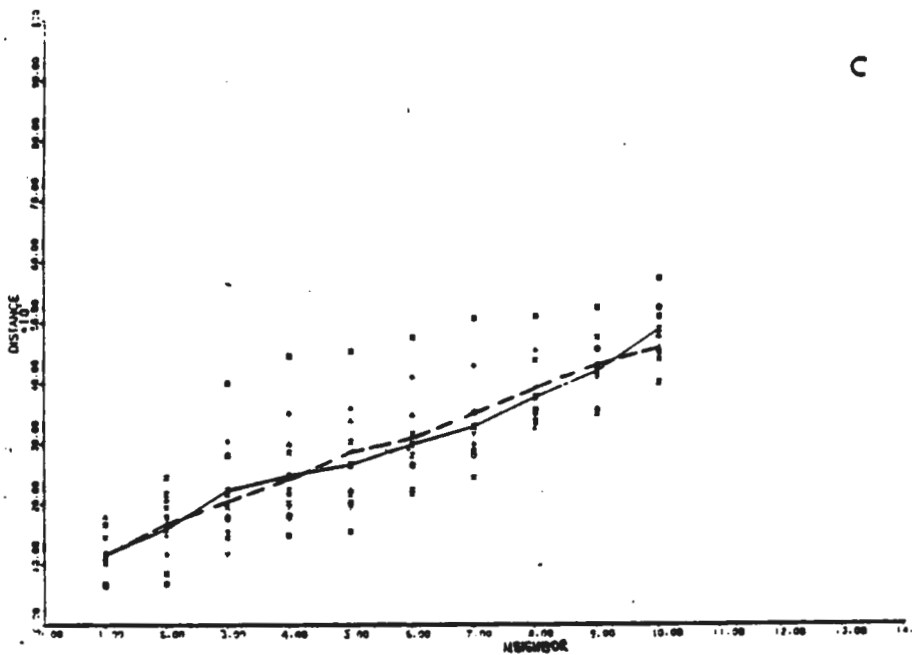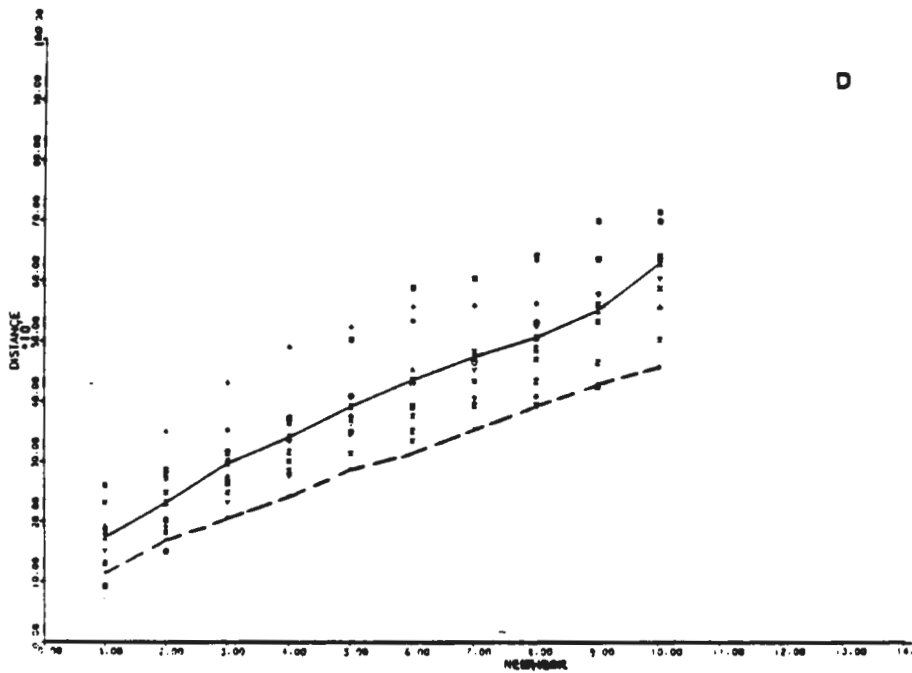
Figure 7. Relative positions, shown from two view-
points, of flock members in trial seven
at five periods in time for which
relative position could be calculated.
Assigned numbers of birds are shown as
seen from above (left plot) and as
seen from the side (right plot). The
X-Y axis has been centered at the
geometric center of the flock in each of
the plots. The arrow at the right of
the X axis indicates the direction of
travel of the flock.
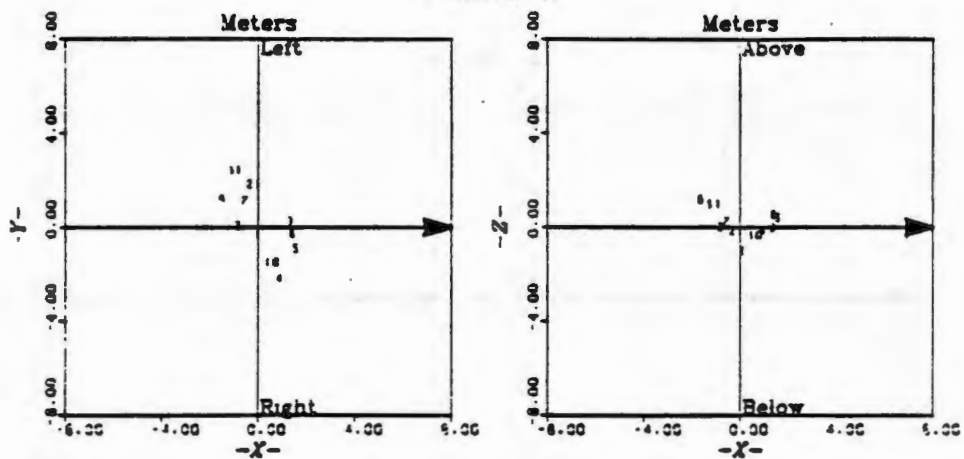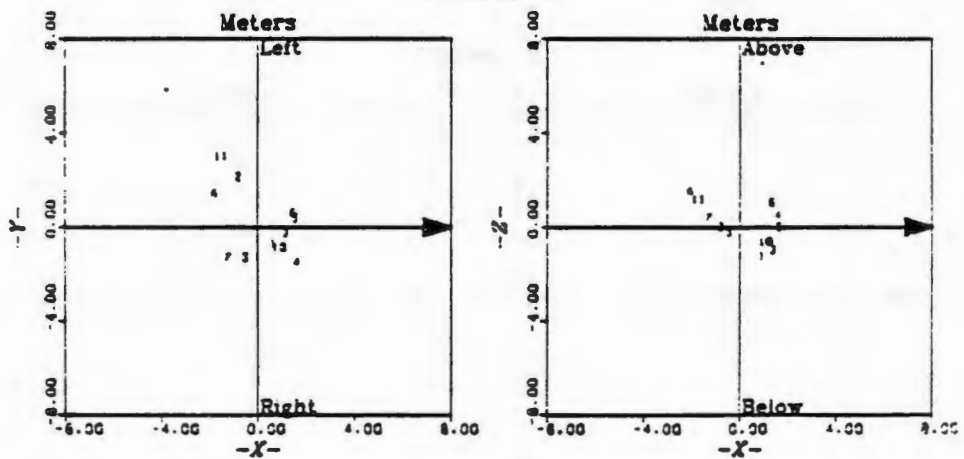
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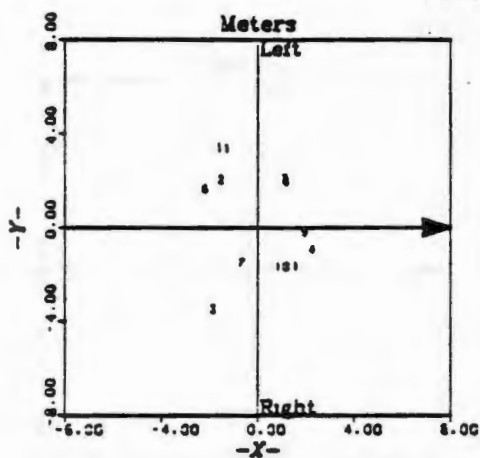
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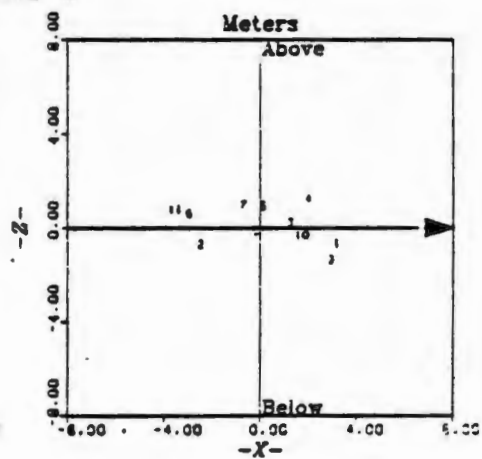
FRAME 4

FRAME 5

FRAME 6
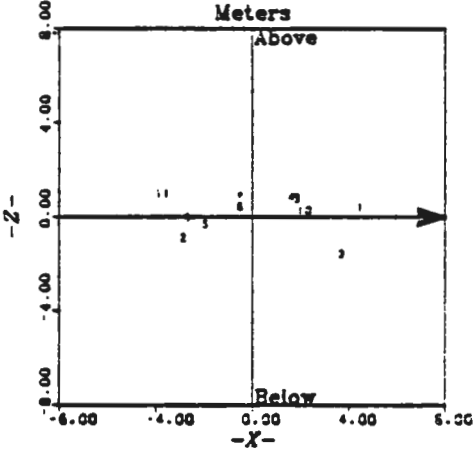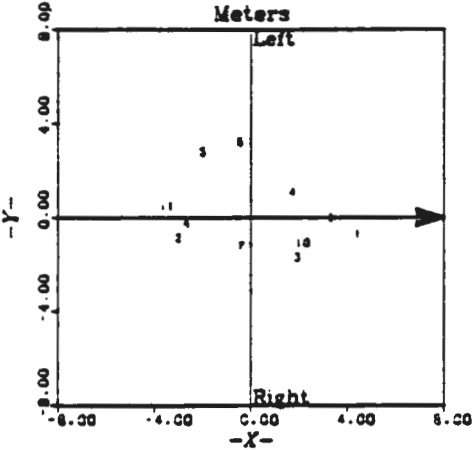
Figure 8. Spearman rank order correlations between
front to back sequence of birds in the
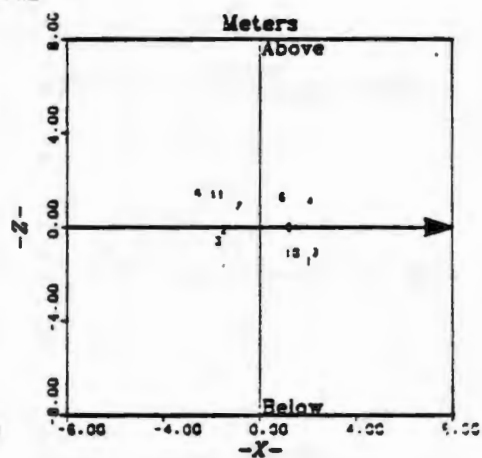flock. Correlation coefficients (ordinate)
are plotted for each of the increasingly
longer time periods separating when the
two rankings of birds used in the corre-
lation were established (abscissa).

Figure 9.   Summary information on flock movements
over time. Figure 9a shows the flock
in trial eight as seen from above for
the eight points in time at which the
flock was photographed. Arrows indicate
the direction of travel of the flock.
Figure 9b shows the changes in elevation
of the geometric center of the flock
over time. Note that the X-Y plane was
elevated approximately 150 cm above
ground level.
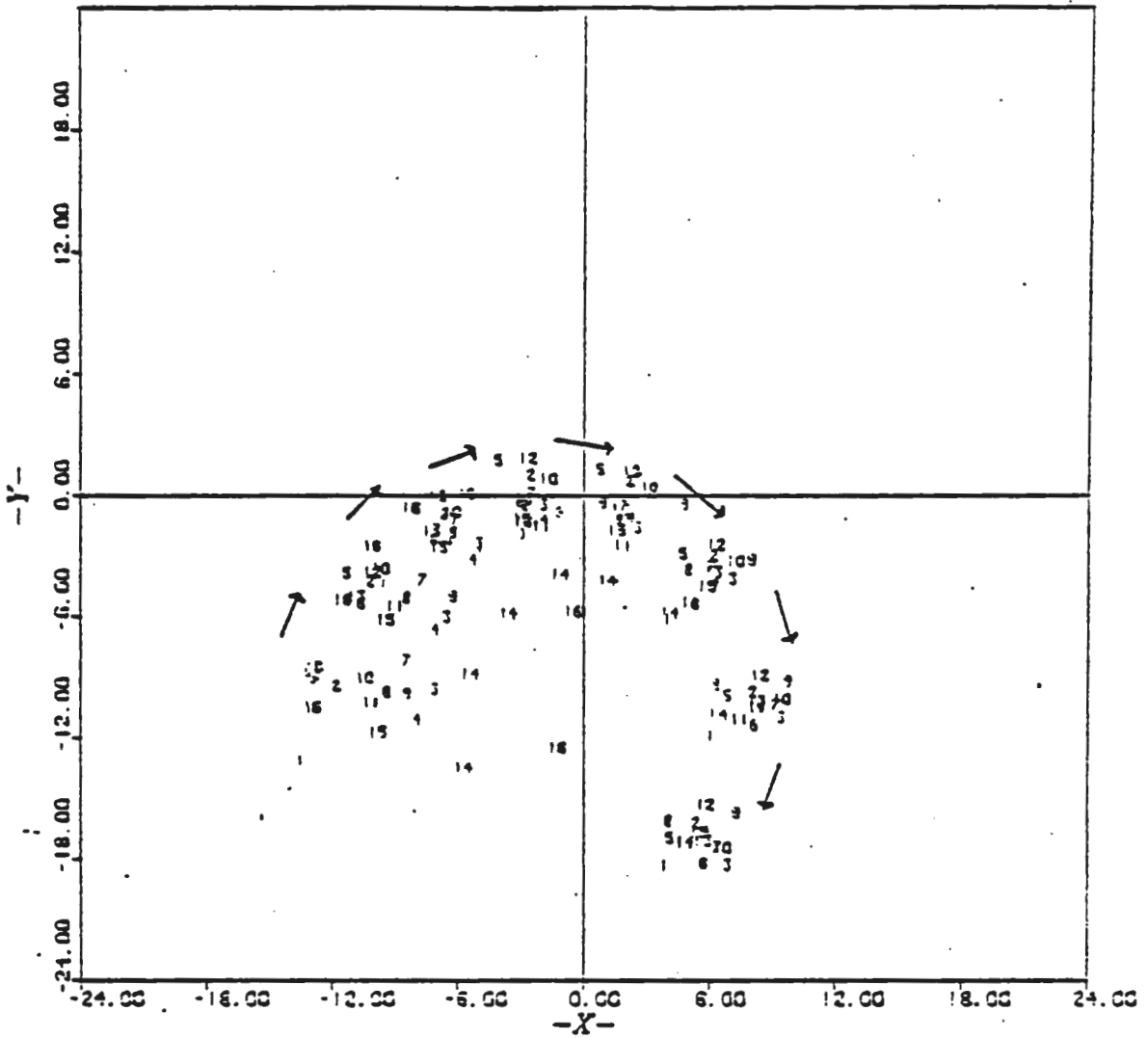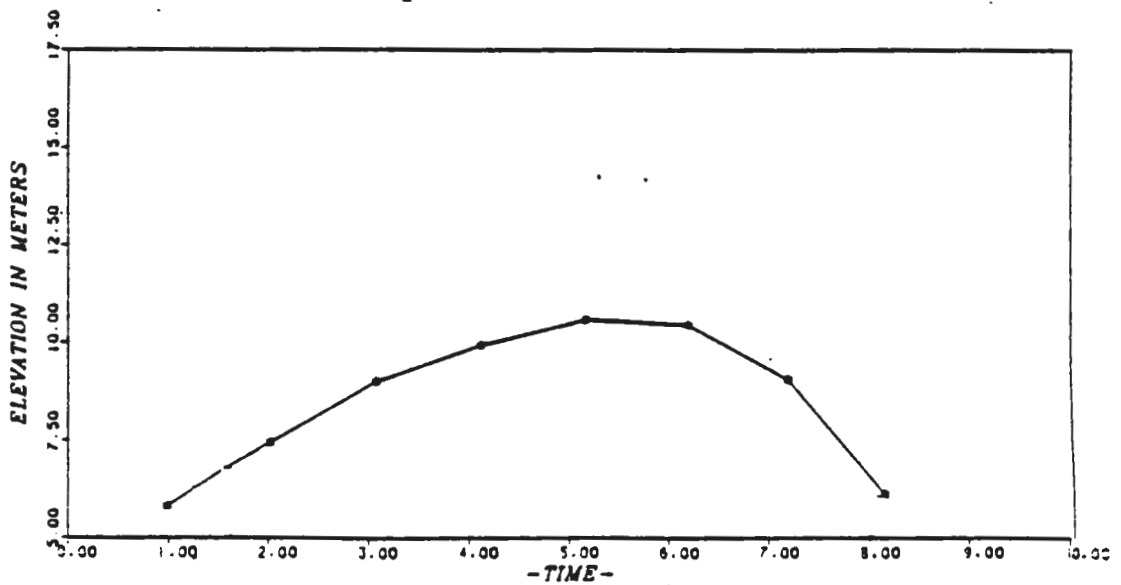
Figure 10. Changes in values for mean distance to
nearest neighbor and mean separation
distance within the flock for the eight
time periods in trial eight. Specific
types of combinations of changes in the
two parameters may indicate different
types of deployment of birds within
the flock (see text for full explanation).
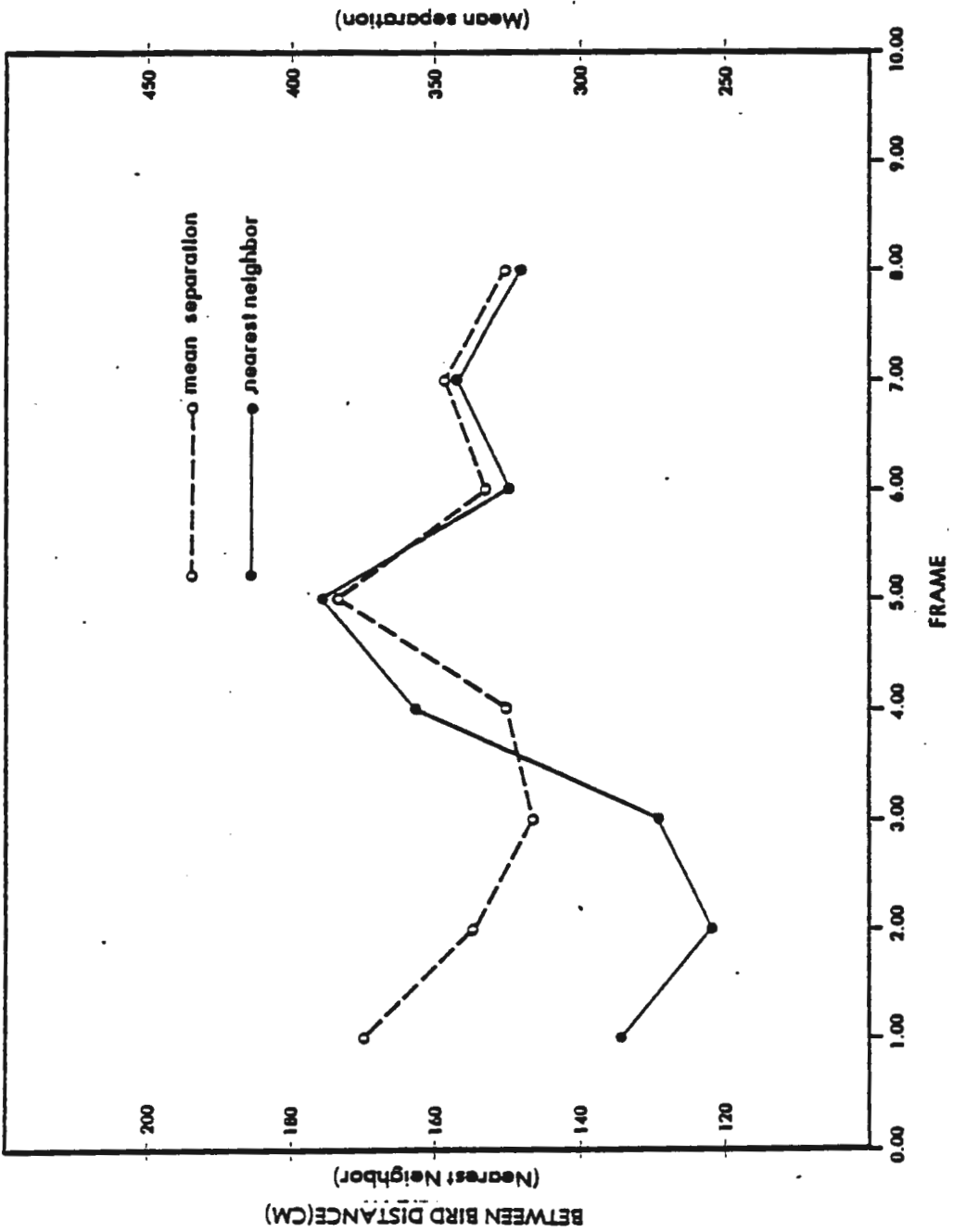
Figure 11. Distances to first through N^{th}
neighbor within the flock are plotted
for each of the time periods at which
the flock in trial eight was photo-
graphed. Figure 11a shows the neighbor
distance distribution for time one,
while Figure 11b shows the distances for
time eight. The solid line in each
plot connects the mean values of the
distributions. The dashed line in all
but the first plot is a trace of the
line which connects mean values at
time one, and appears so that changes
in distributions over time may be more
readily seen.
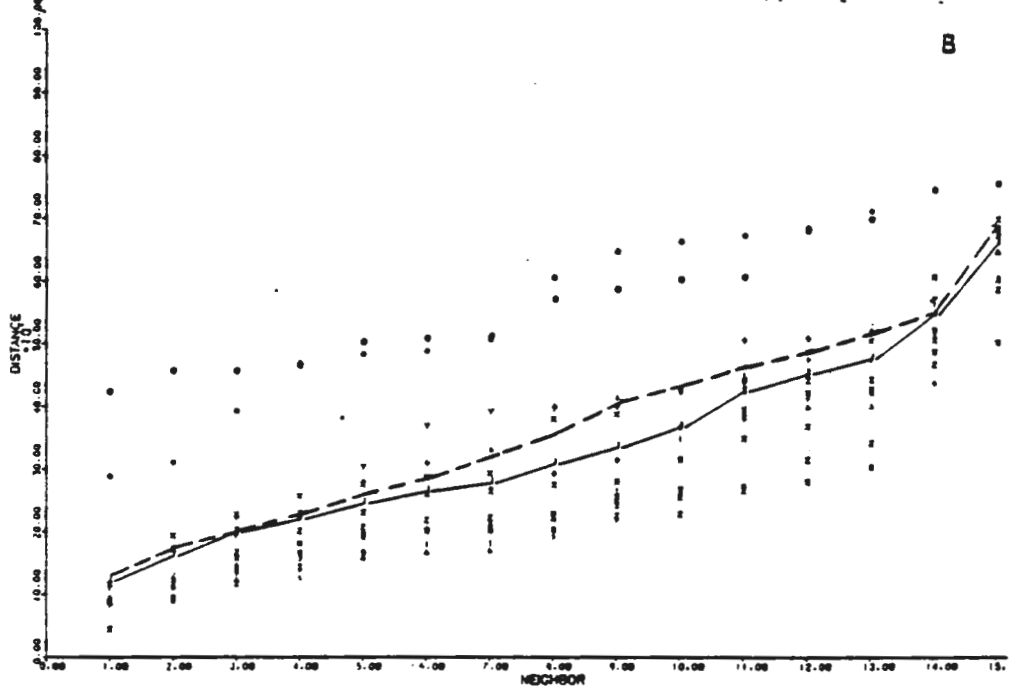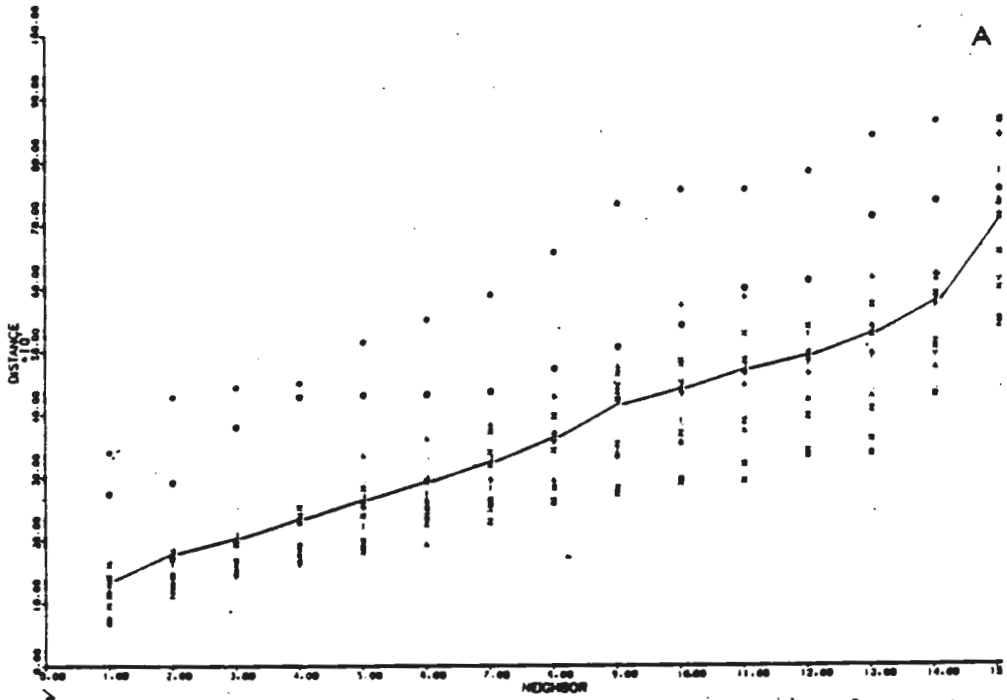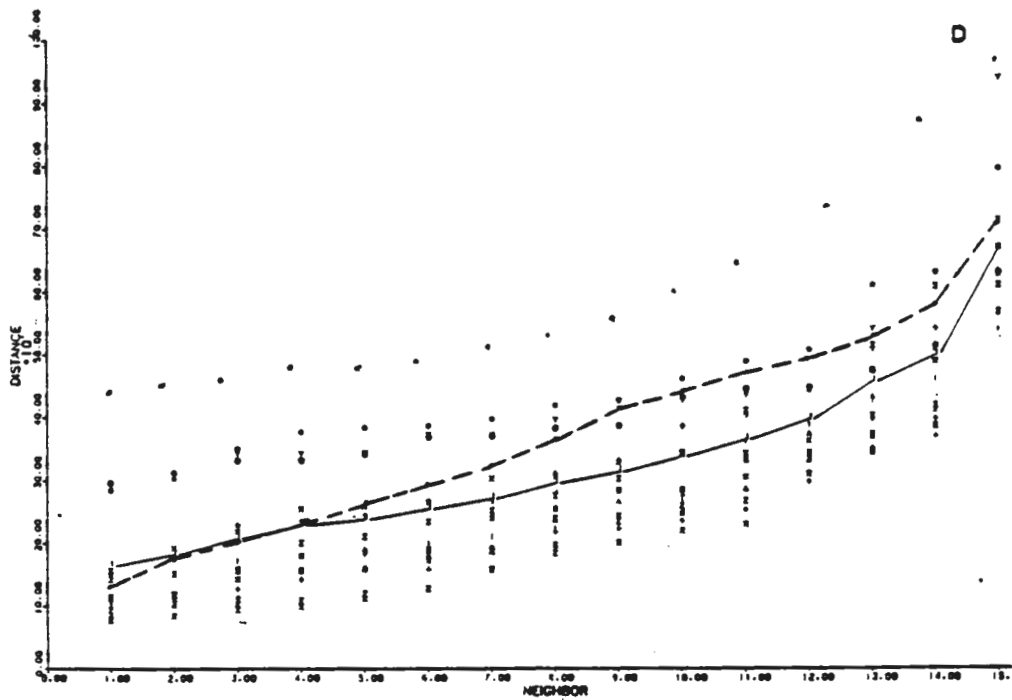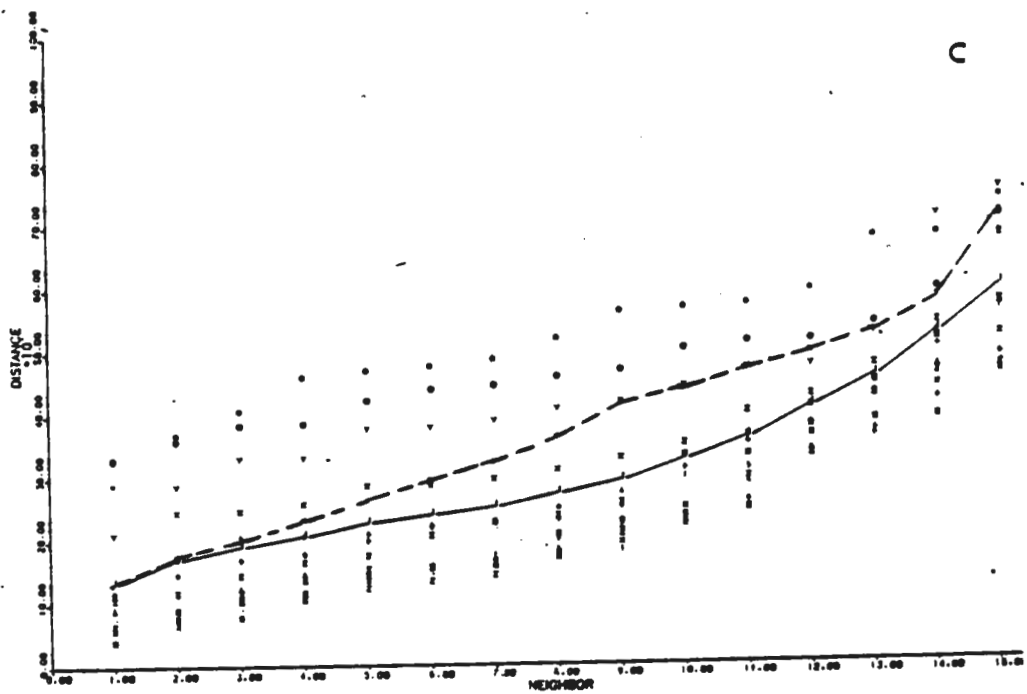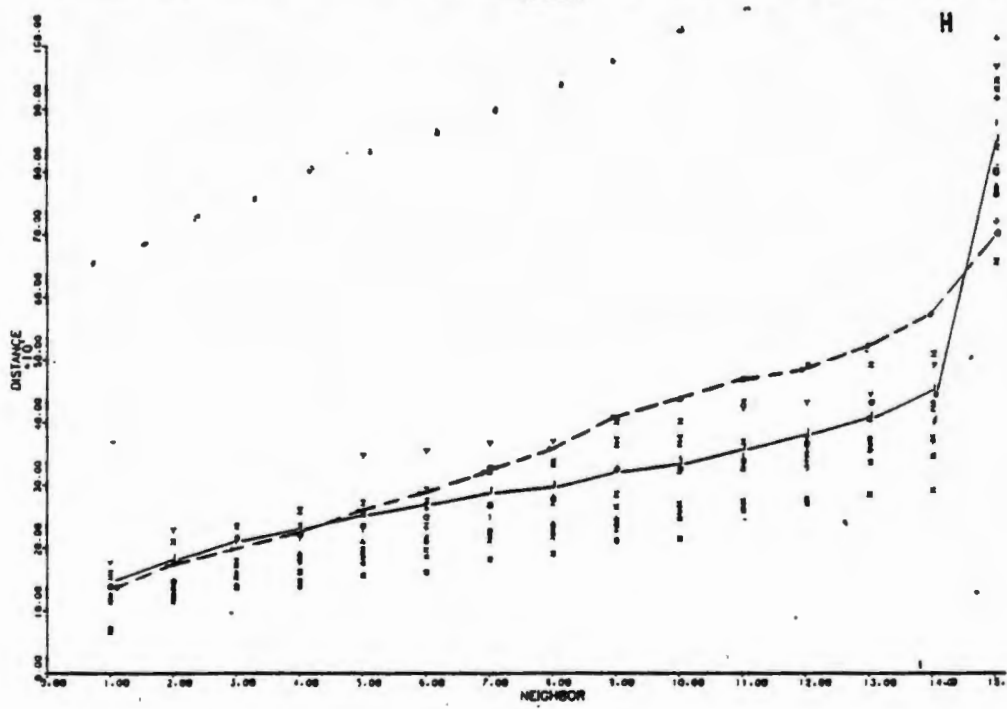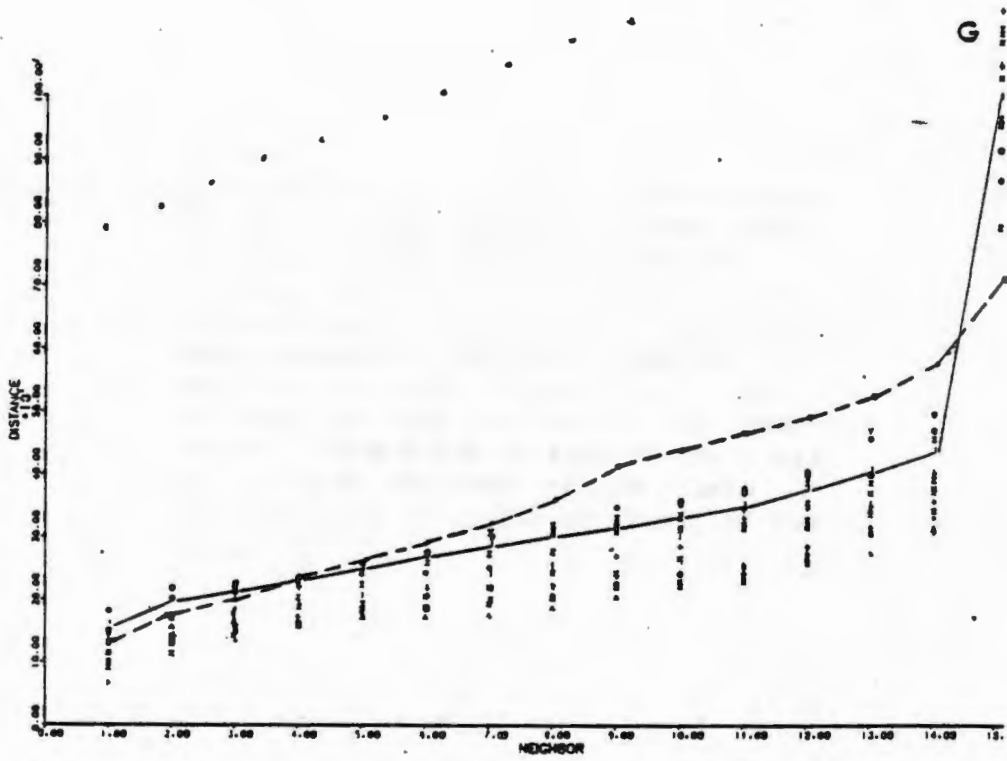
Figure 12. Relative positions, shown from two view-
points, of flock members in trial eight
at seven periods in time for which
relative positions could be calculated.
Assigned numbers of birds are shown as
seen from above (left plot) and as
seen from the side (right plot). The
X-Y axis has been centered at the geometric
center of the flock in each of the plots.
The arrow at the right of the X axis
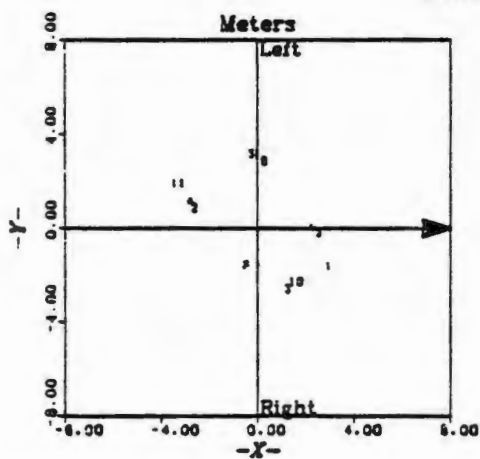indicates the direction of travel of the
flock.
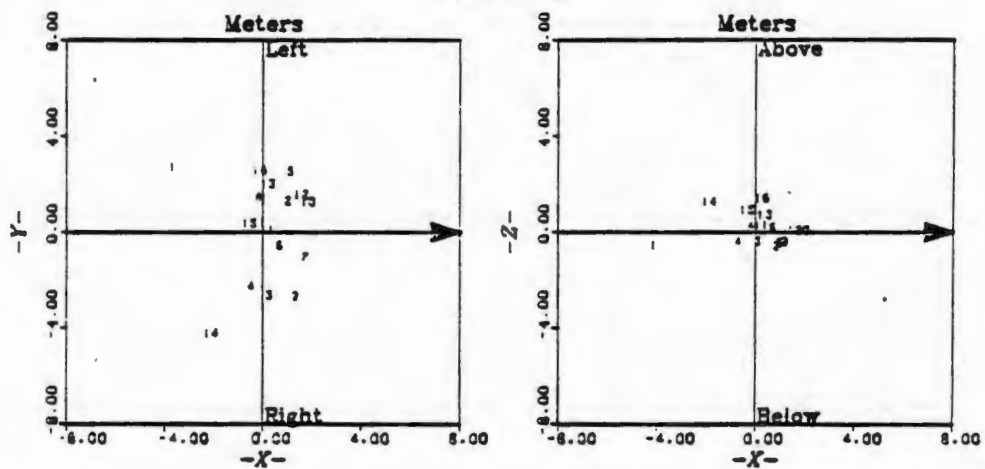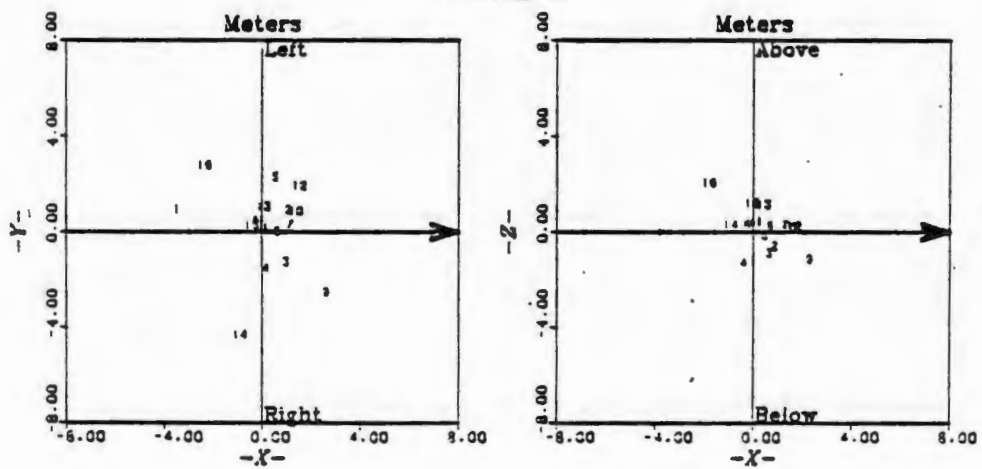
FRAME 2
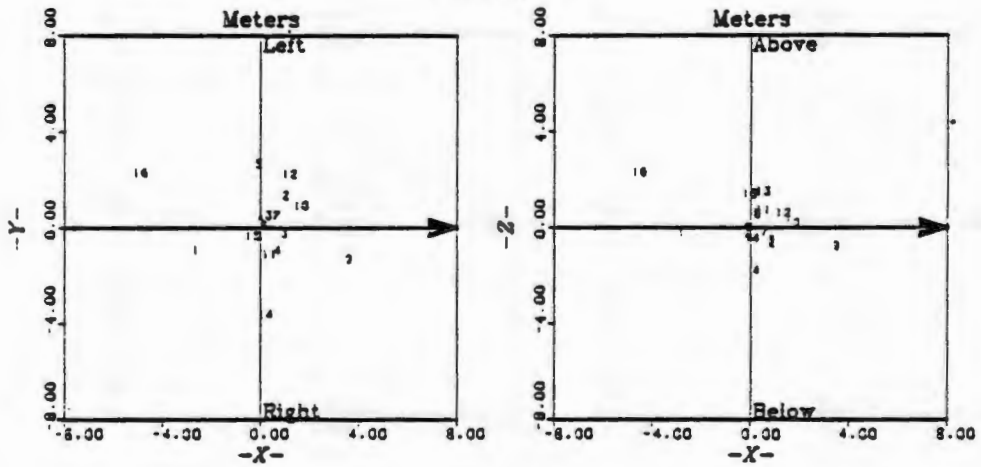
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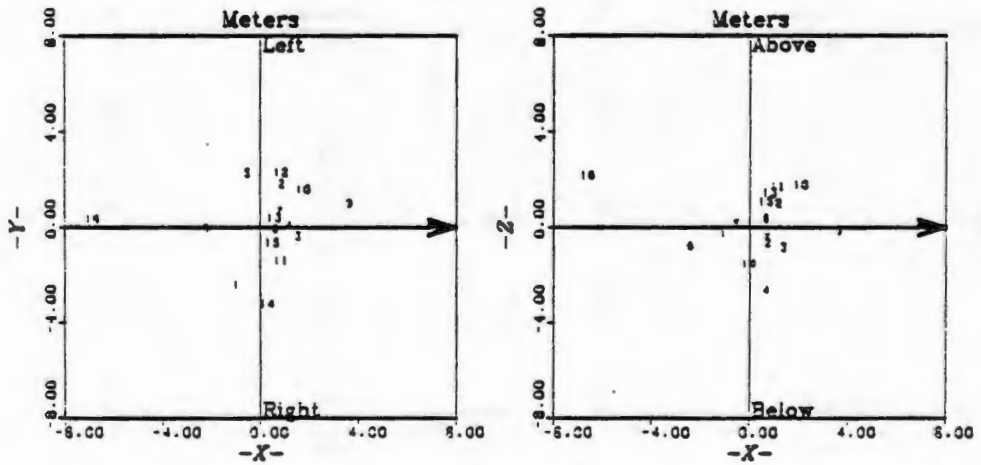
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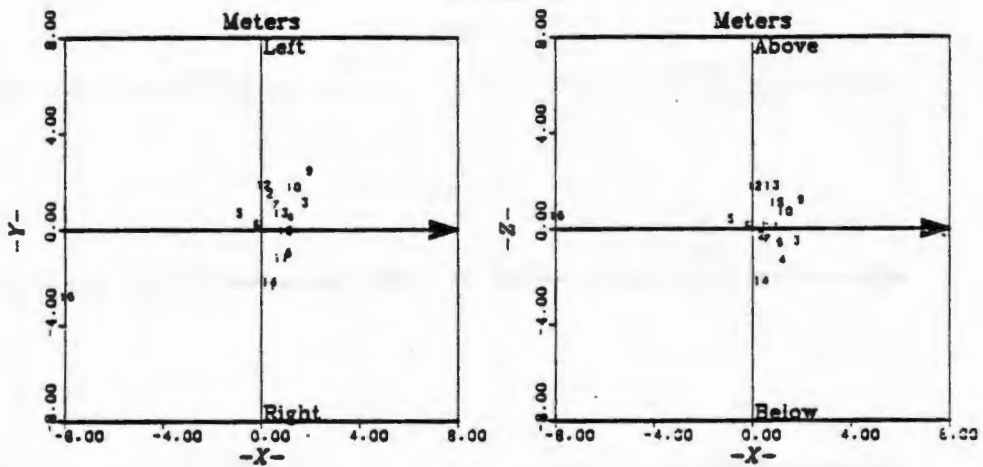
FRAME 5

FRAME 6

FRAME 7
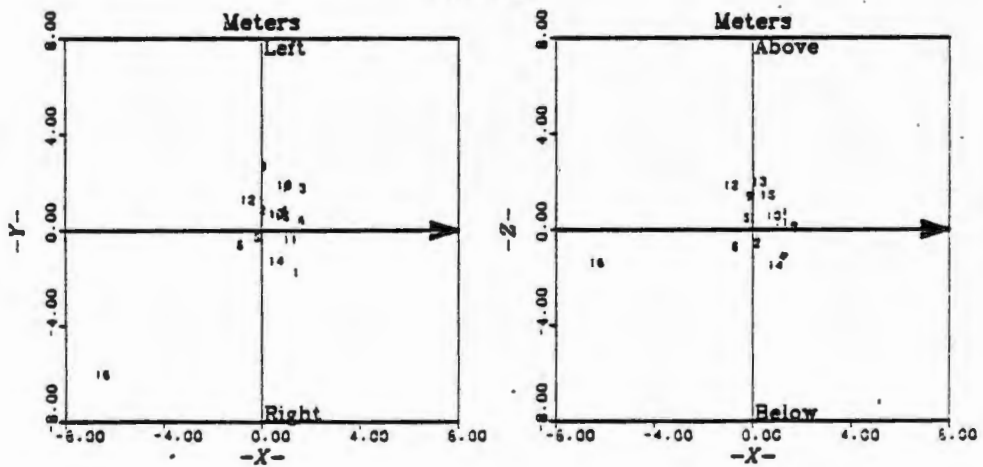
FRAME 8
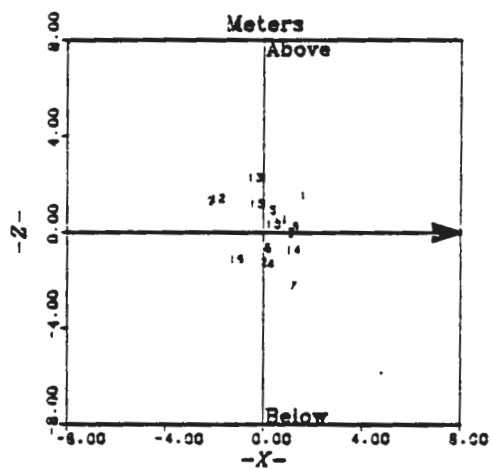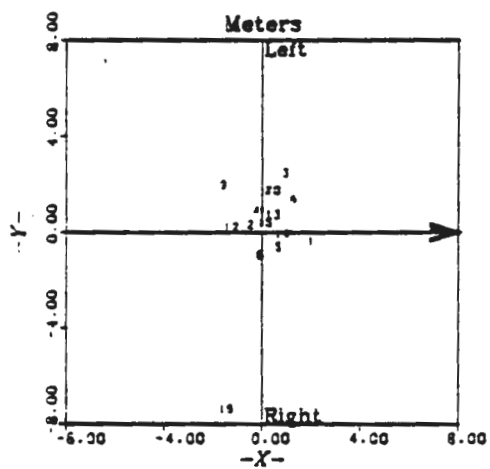
Figure 13. Spearman rank order correlations between front to back sequence of birds in the flock. Correlation coefficients (ordinate) are plotted for each of the increasingly longer time periods separating when the two rankings of birds used in the correlation was established (abscissa).
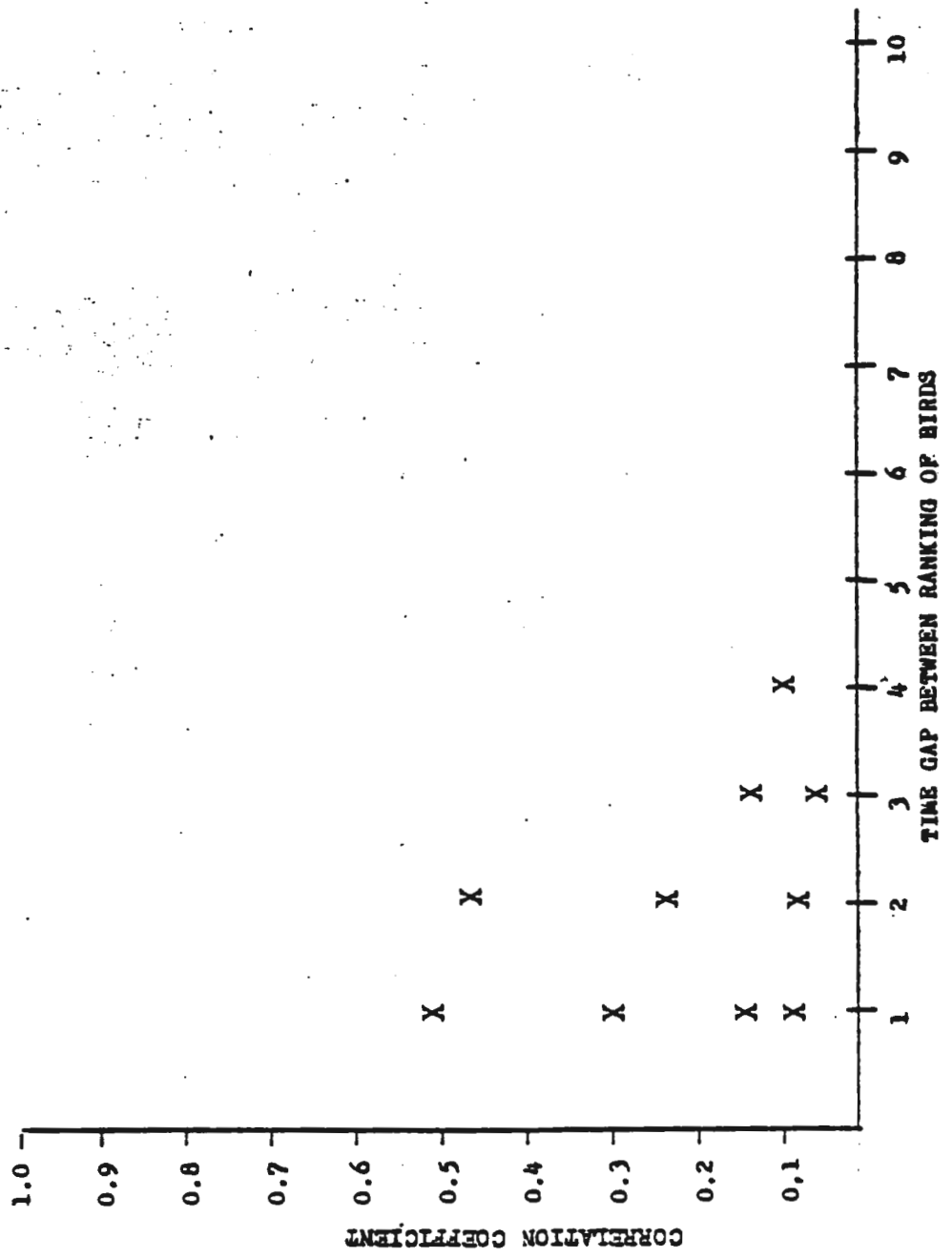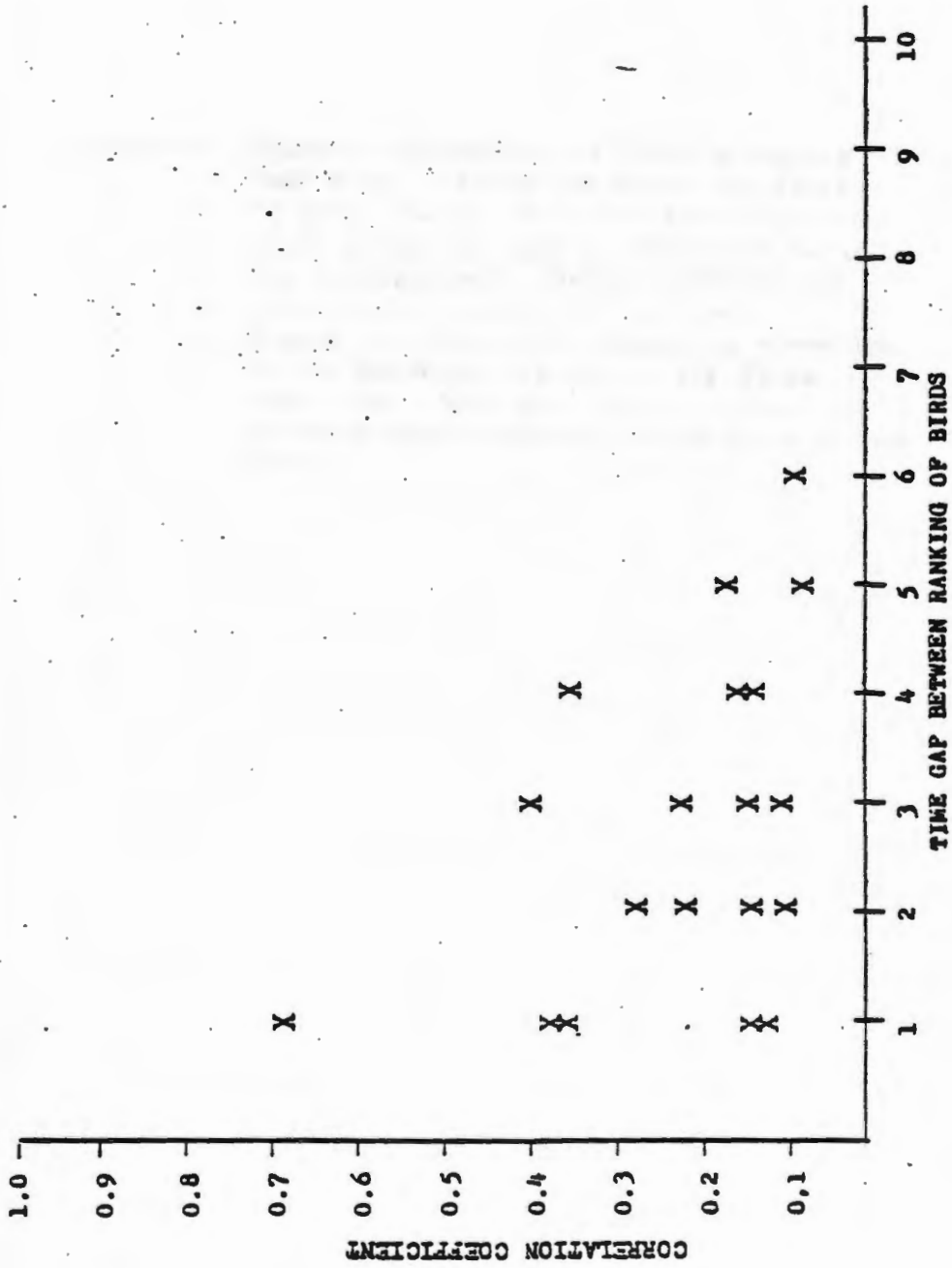
Figure 14. Summary information on flock movements
over time. Figure 14a shows the flock
in trial two as seen from above for the
seven points in time at which the flock
was photographed. Arrows indicate the
direction of travel of the flock.
Figure 14b shows the changes in elevation
of the geometric center of the flock
over time. Note that the X-Y plane was
elevated approximately 150 cm above ground
level.

A
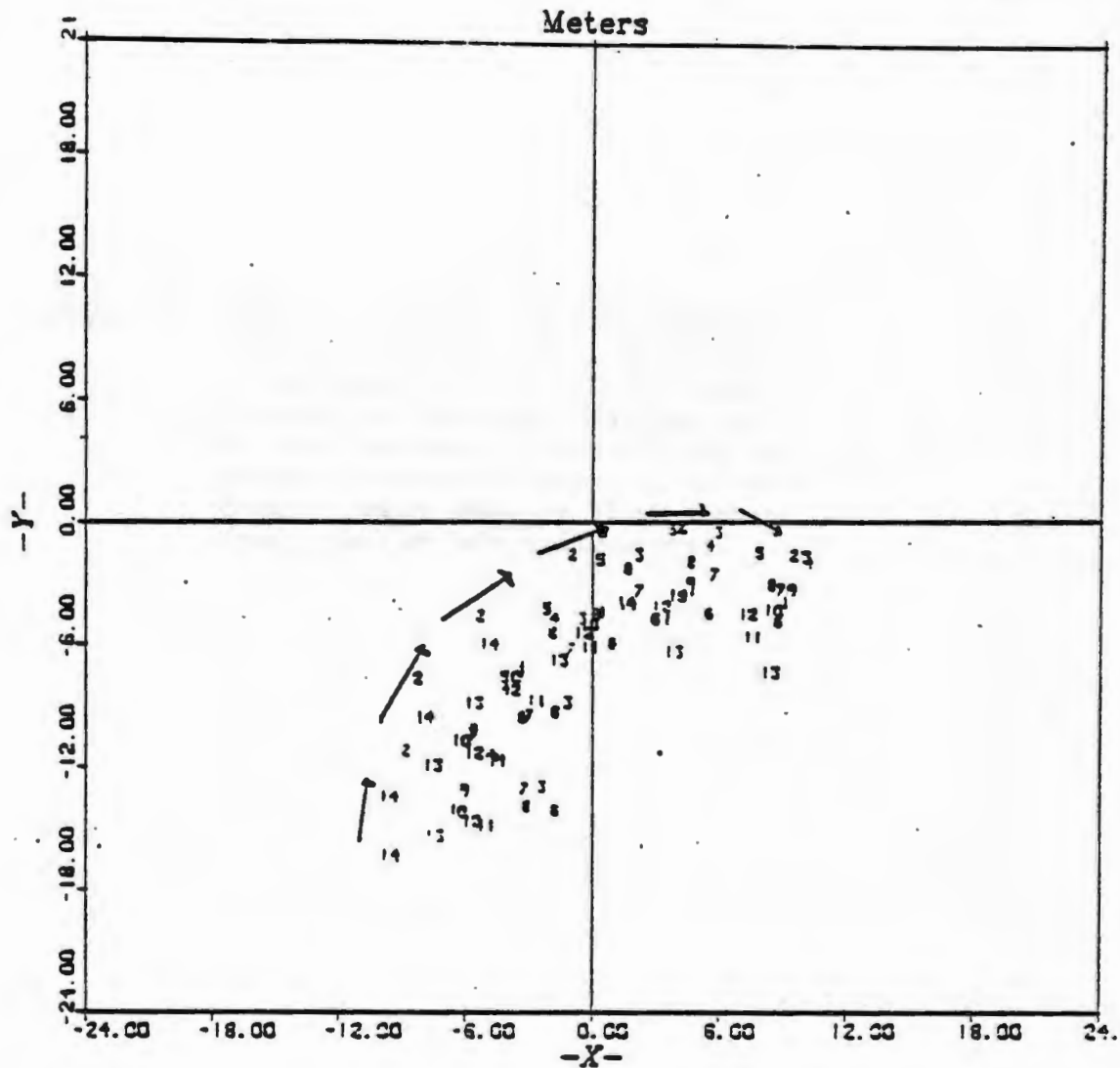
B
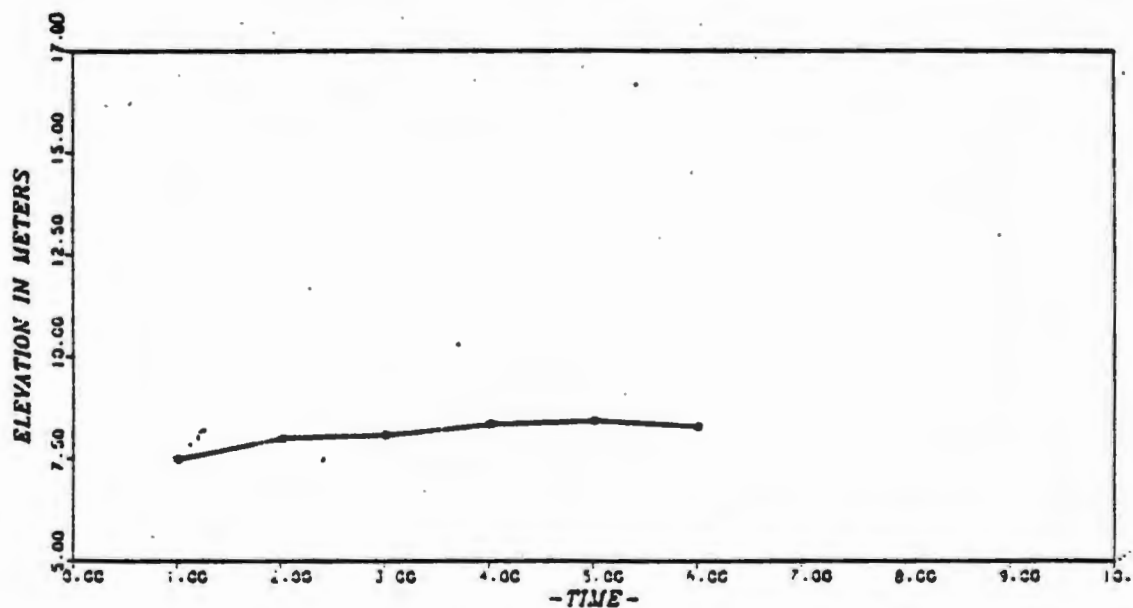
Figure 15. Changes in values for mean separation
distance and mean distance to first
nearest neighbor for the six time
periods in trial two. Various types
of combinations of change in the two
parameters are indicative of specific
types of deployment of flock members
(see text for full explanation).
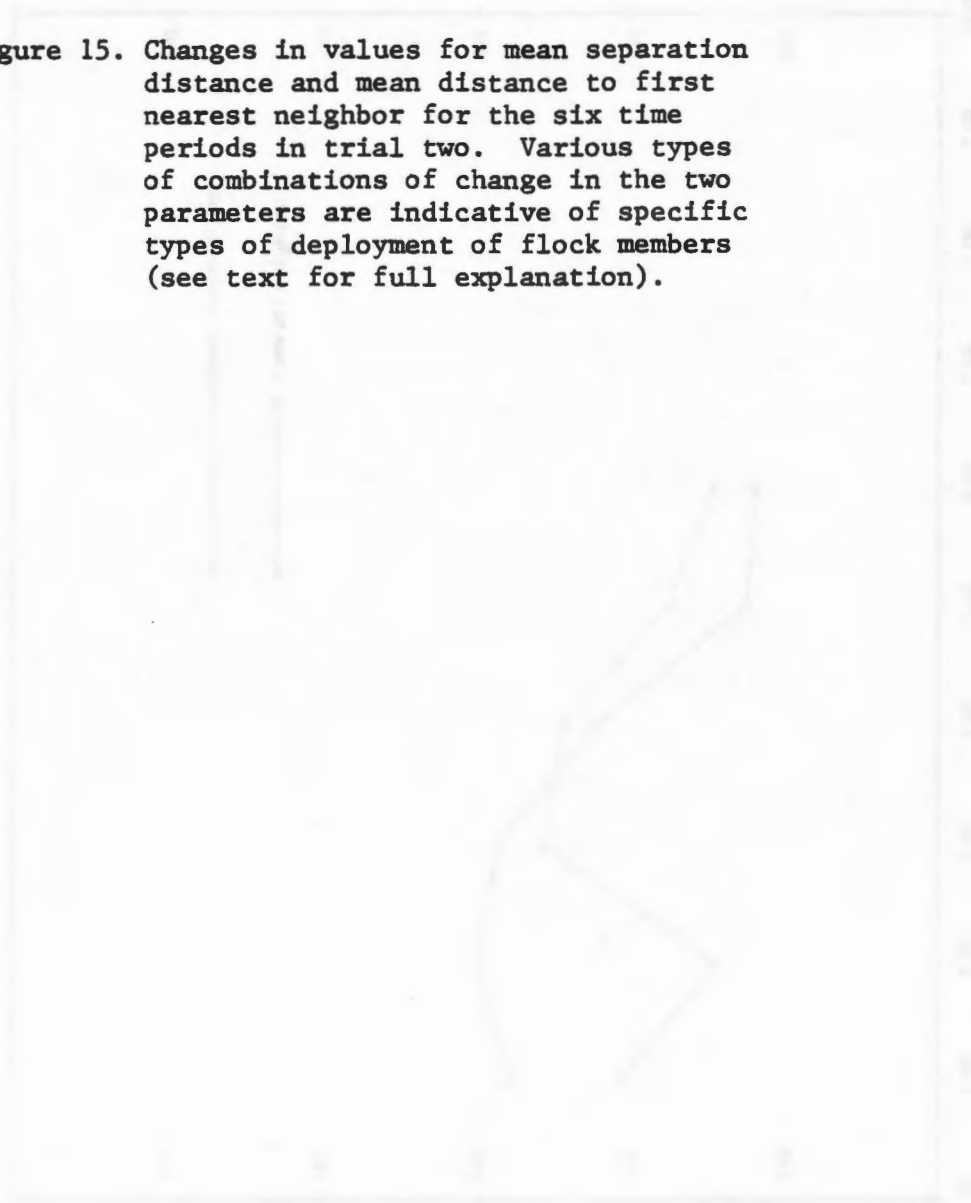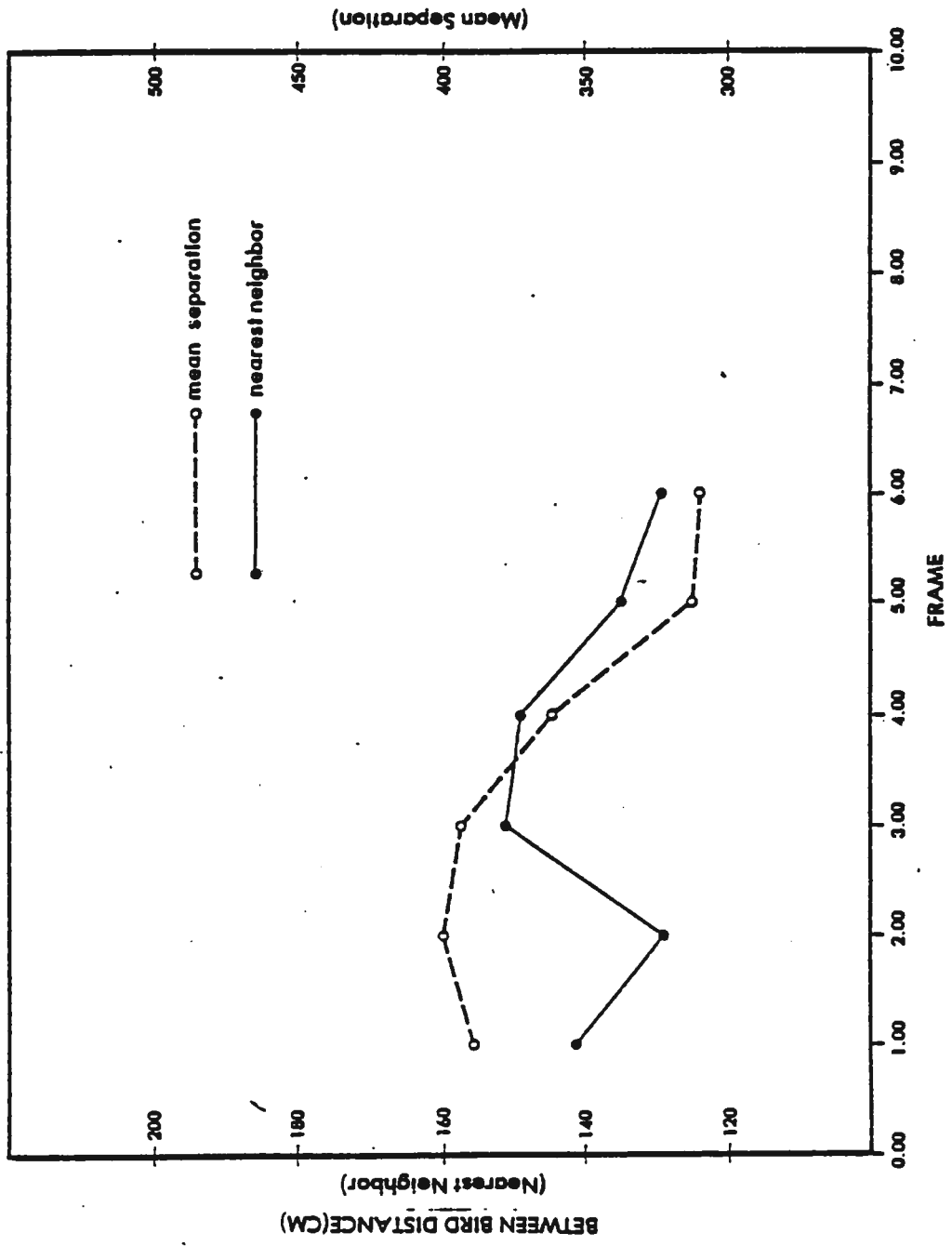
Figure 16. Distances to first through N^{th}
            neighbor within the flock are plotted
            for each of the time periods at which
            the flock in trial two was photographed.
            Figure 16a shows the neighbor distance
            distribution for time one, while
            Figure 16f shows the distances at time
            six. The solid line in each plot
            connects the mean values of the distri-
            butions. The dashed line in all but
            the first plot is a trace of the line
            which connects mean values at time
            one, and appears so that changes in
            distributions over time may be more
            readily seen.

A

B

C

D
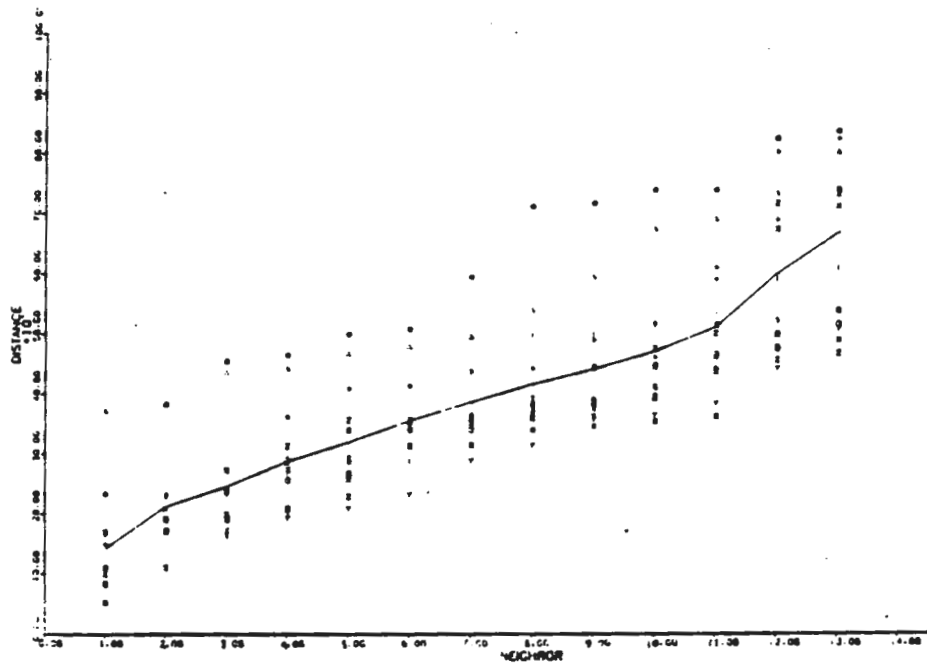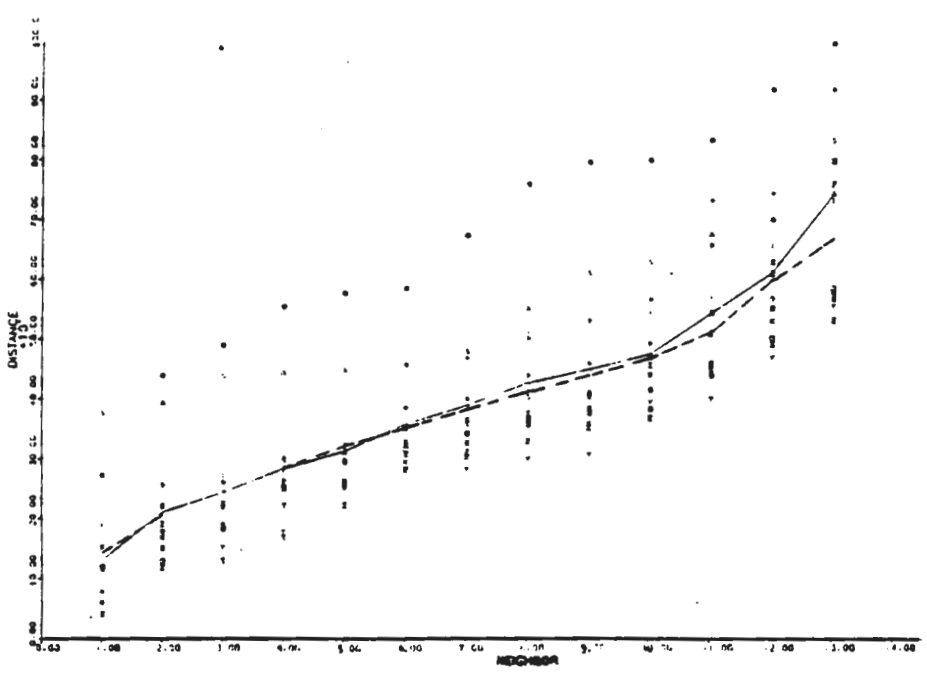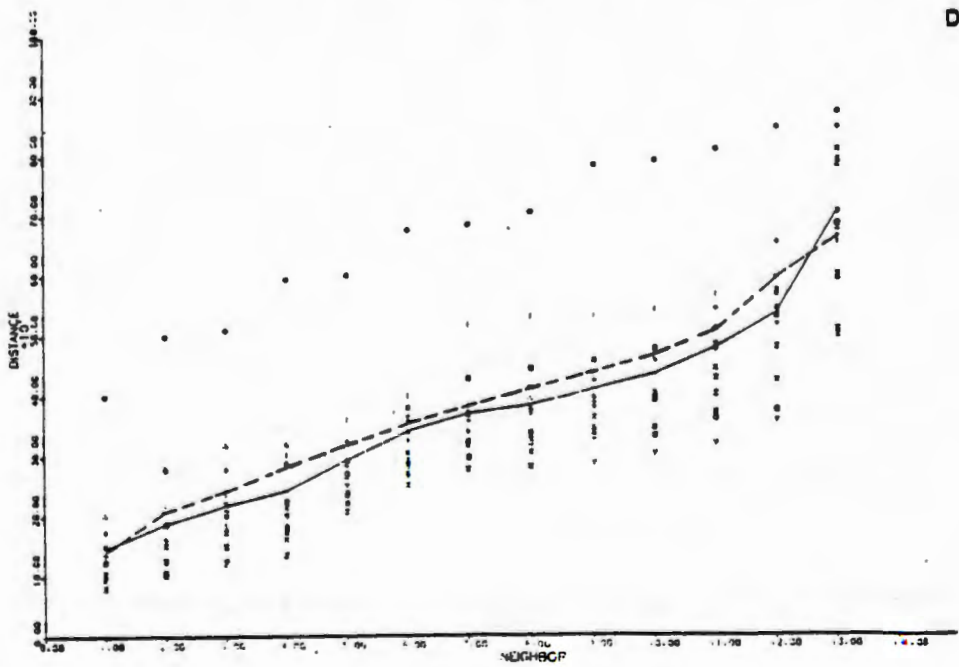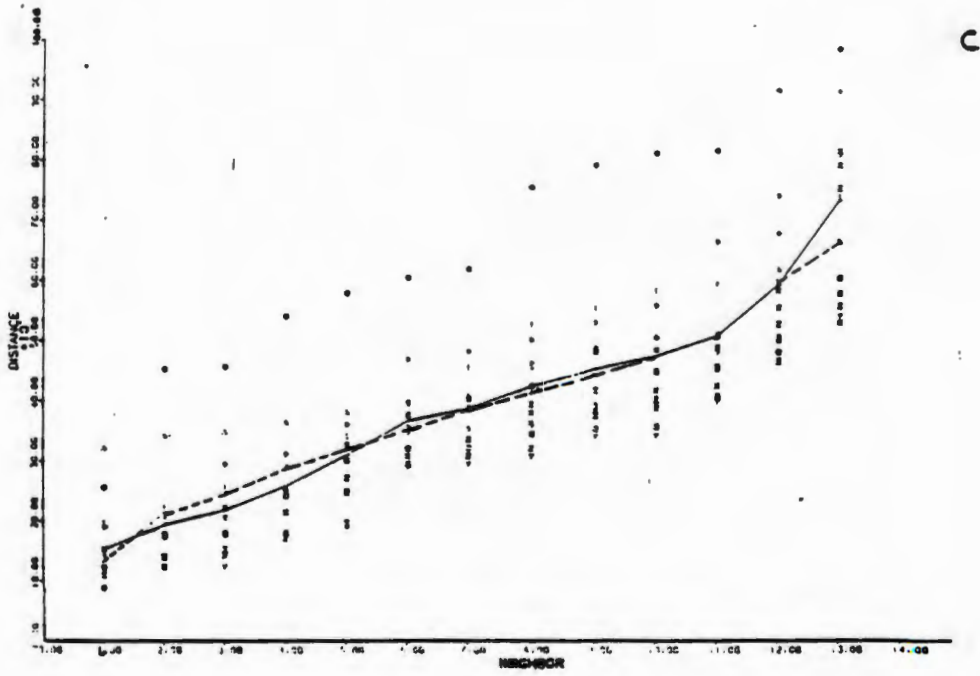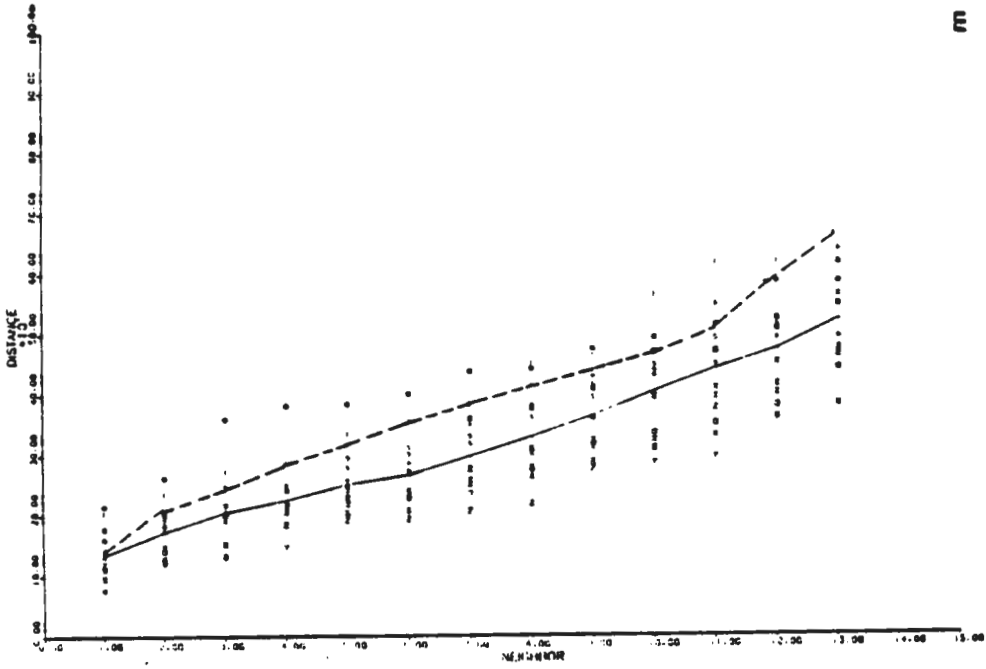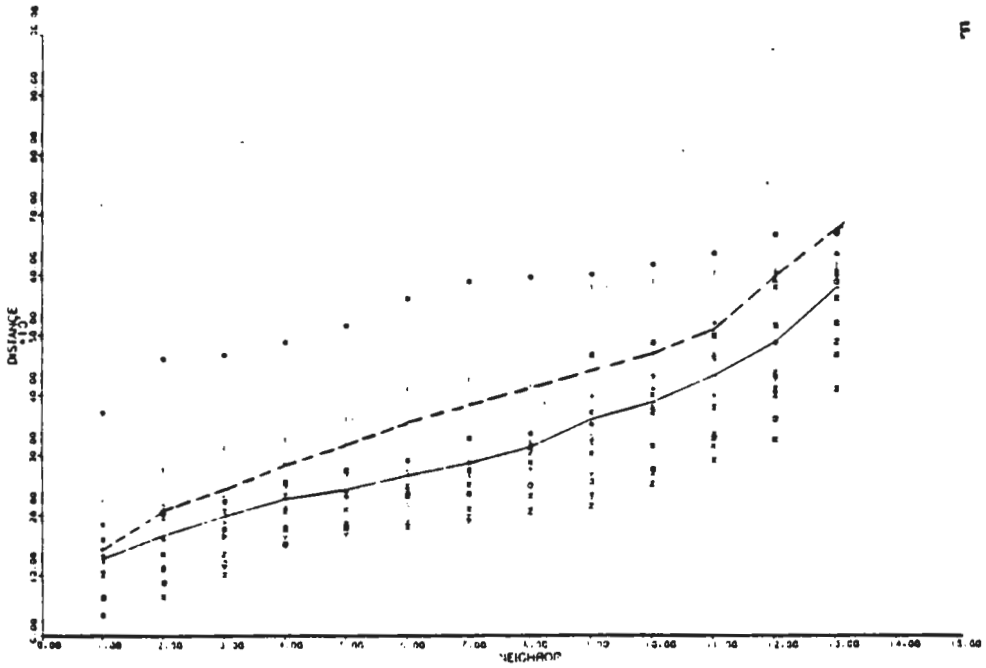
Figure 17. Relative positions, shown from two view-
points, of flock members in trial two
at five periods in time for which relative
positions could be calculated.
Assigned numbers of birds are shown as seen
from above (left plot) and as seen
from the side (right plot). The X-Y axis
has been centered at the geometric center
of the flock in each of the plots. The
arrow the right of the X axis indicates the
direction of travel of the flock.
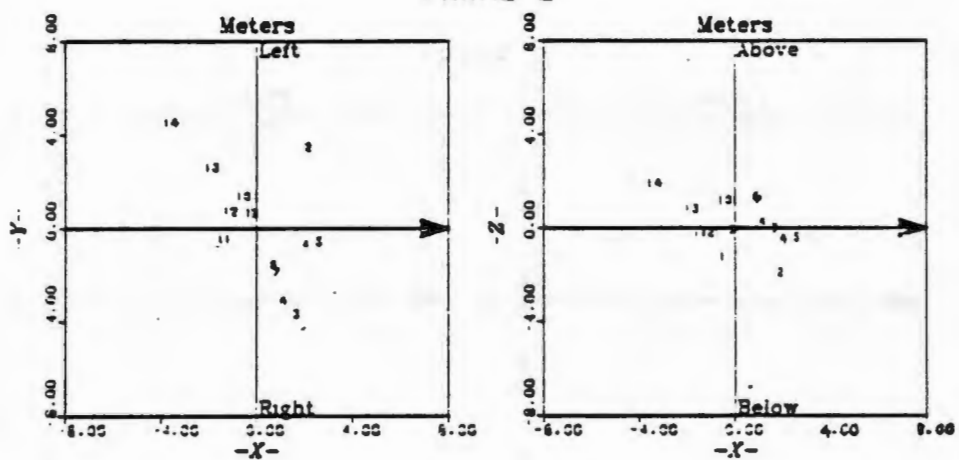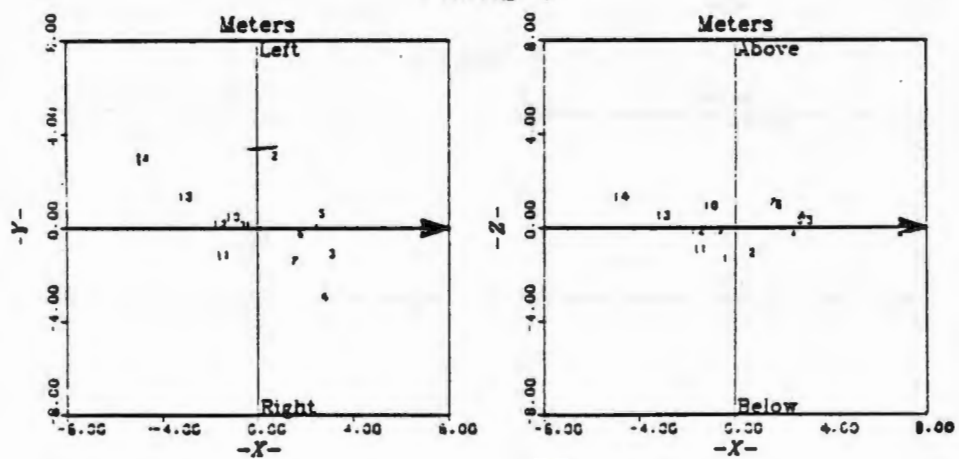
FRAME 2
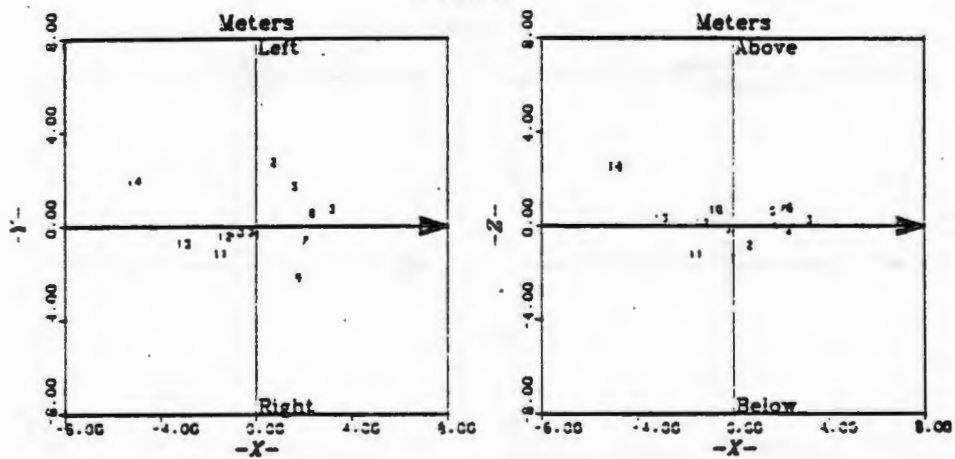
FRAME 3
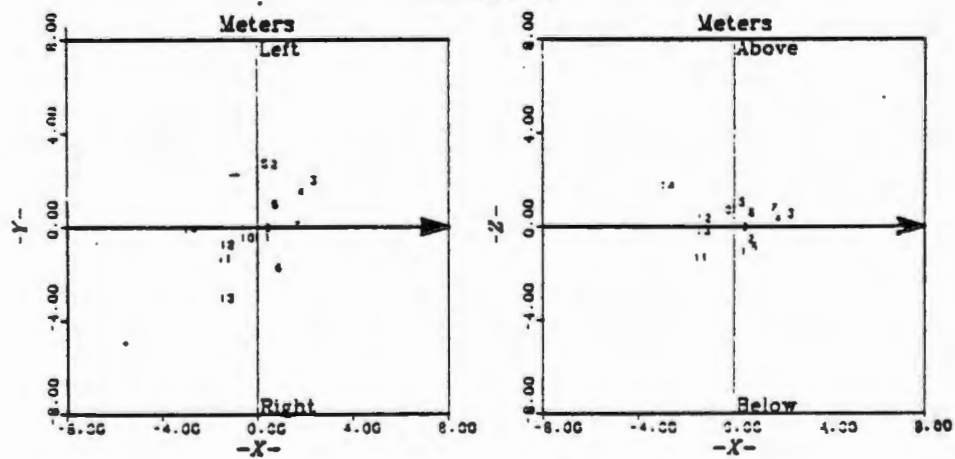
FRAME 4

FRAME 5

FRAME 6
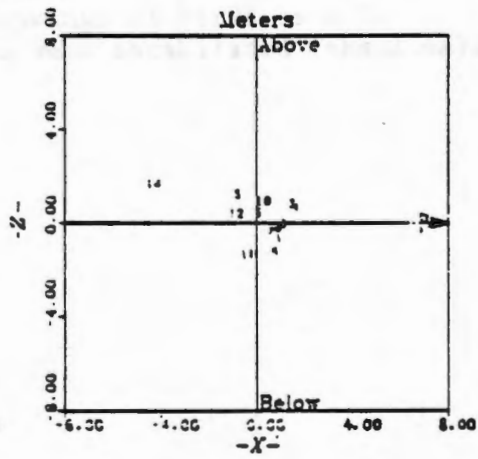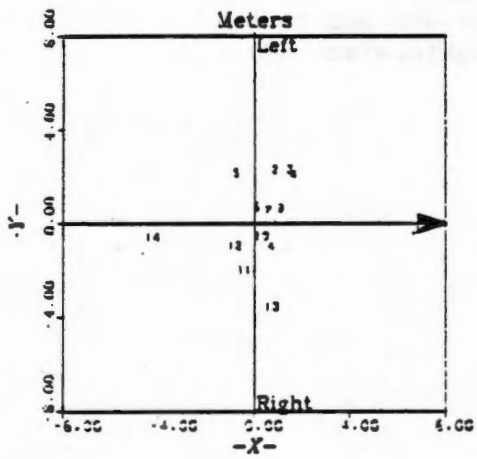
Figure 18.   Spearman rank order correlations between
front to back sequence of birds in the
flock.   Correlation coefficients
(ordinate) are plotted for each of the
increasingly longer time periods separating
when the two rankings of birds used in
the correlation were established (abscissa).

TIME GAP BETWEEN RANKING OF BIRDS

CORRELATION COEFFICIENT
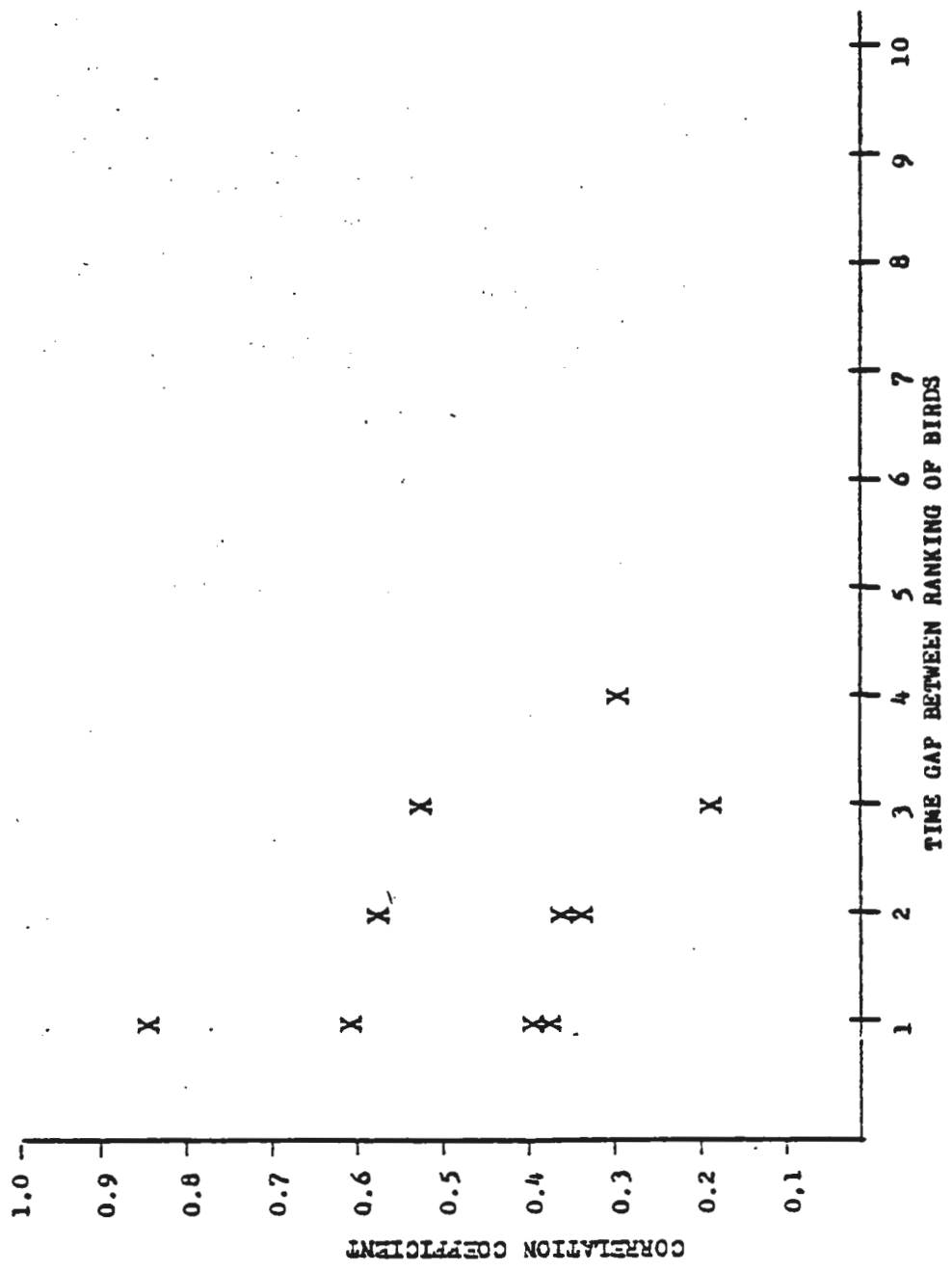
Figure 19.   Summary data on turning in flocks. A
             table is listed for each trial which
             shows the mean flight speed maintained
             by birds in the flock between sequential
             time periods, and the angle of turn
             described by the flock during the same
             time period. Two plots are shown for each
             trial, which show the average flight
             speed and changes in elevation of the
             geometric center of the flock over time.
             Figures 19a through 19e show tables and
             plots for trials two, six, eight, seven,
             and nine respectively.

TIME	SPEED (km/hr)	ANGLE OF TURN
1-2	18.9	—
2-3	20.3	26°
3-4	21.9	19°
4-5	22.0	28°
5-6	21.4	26°
average	21.3	99° -total

a

TIME	SPEED (km/hr)	ANGLE OF TURN
1-2	23.8	—
2-3	16.7	21°
3-4	16.7	29°
4-5	16.3	46°
5-6	16.2	19°
6-7	17.0	37°
7-8	18.6	31°
average	18.22	178° -total
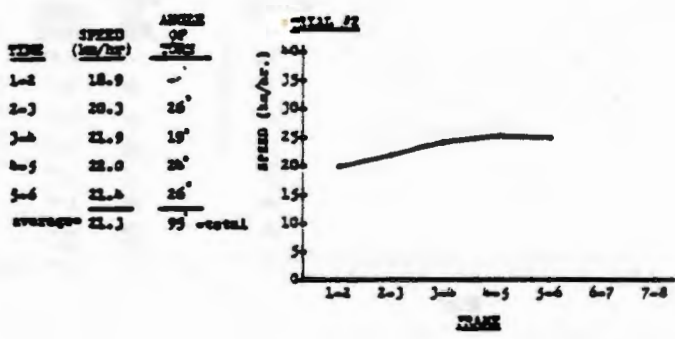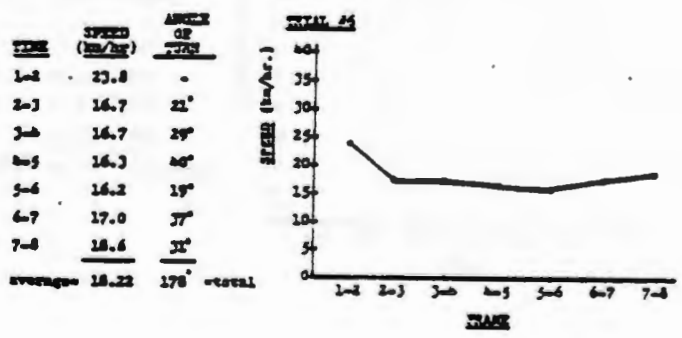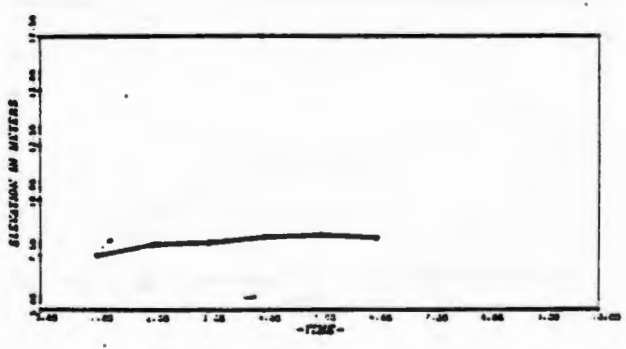
b
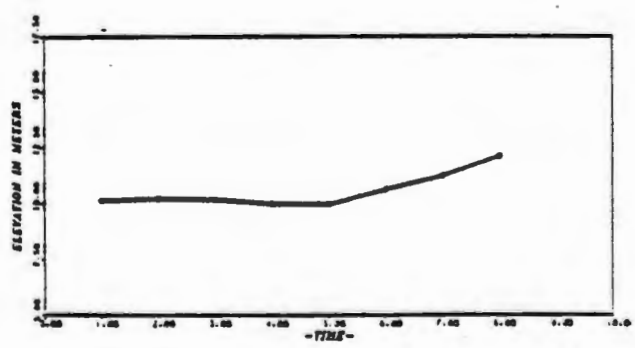
TIME	SPEED (km/hr)	ANGLE OF TURN
1-2	27.0	-
2-3	23.6	20°
3-4	22.1	22°
4-5	22.8	33°
5-6	25.9	30°
6-7	30.3	25°
7-8	39.0	46°
averages	27.7	172° total

TRIAL 28
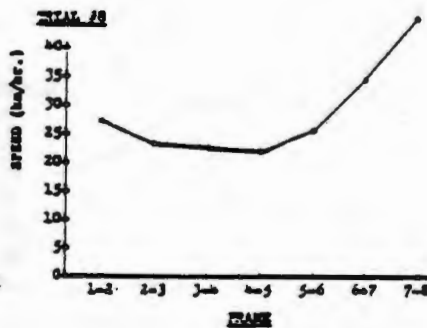
c
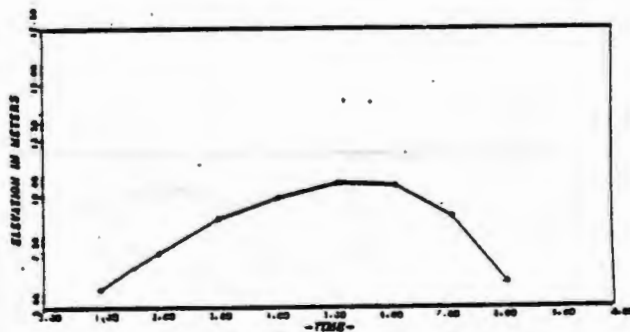
TIME	SPEED (km/hr)	ANGLE OF TURN
1-2	33.0	-
2-3	34.6	29°
3-4	44.1	32°
4-5	43.6	30°
5-6	43.0	25°
averages	43.7	116° total

TRIAL 29

d

TIME	SPEED (km/hr)	ANGLE OF TURN
1-2	29.7	-
2-3	33.7	22°
3-4	42.3	30°
4-5	39.8	25°
averages	36.4	77° total
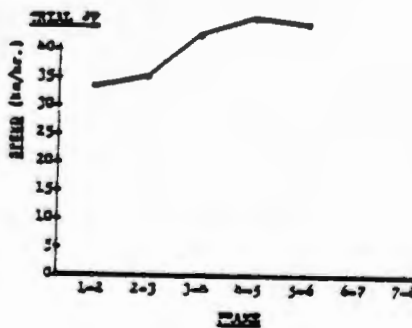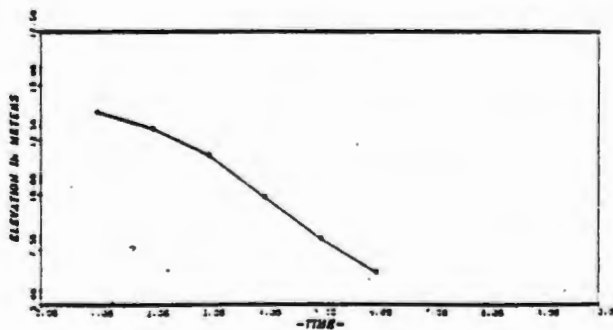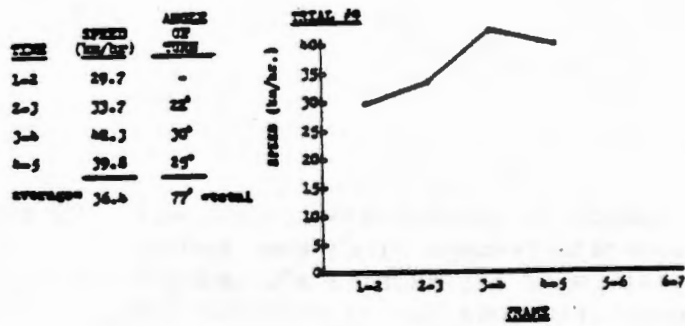
e
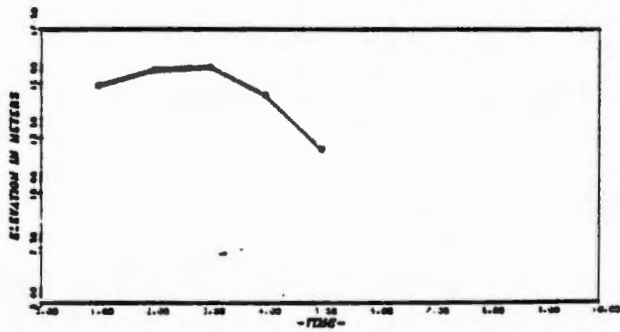
Figure 20. Frequency distributions of pigeon first,
second, and third nearest distances.
Figures 20a through 20e show distributions
for birds in trials two, six, seven,
eight, and nine respectively.

TRIAL 2

First Nearest Neighbor

Second Nearest Neighbor

Third Nearest Neighbor
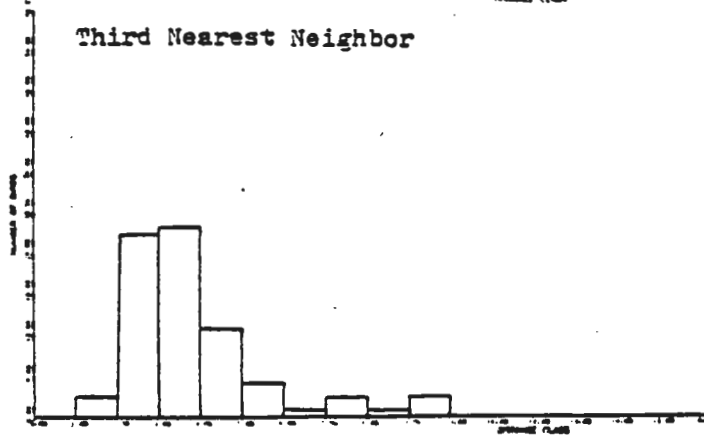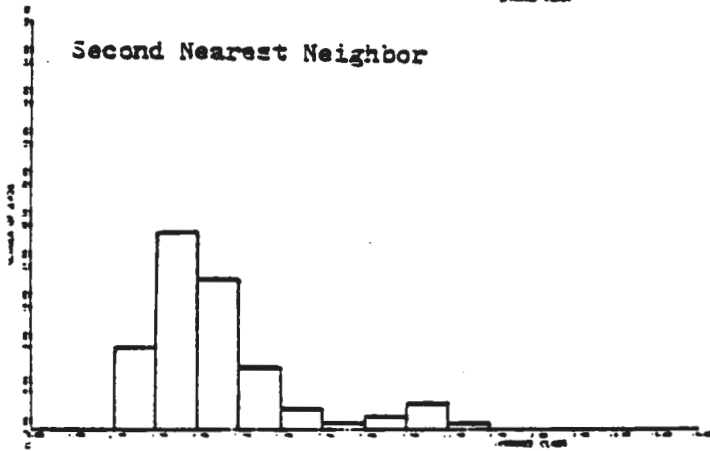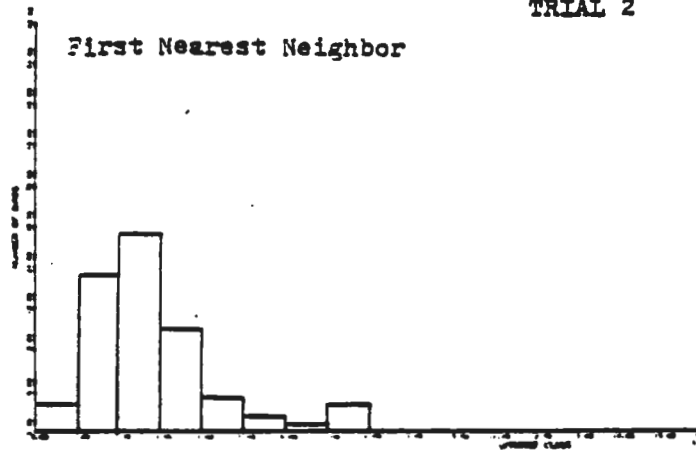
TRIAL 6

First Nearest Nieghbor

b
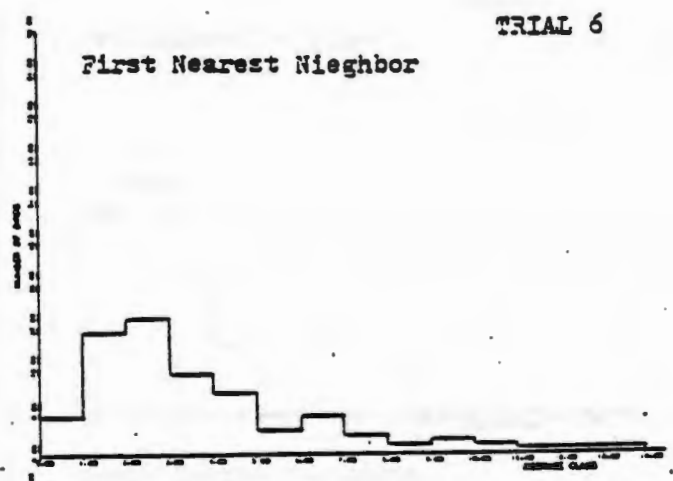
Second Nearest Neighbor
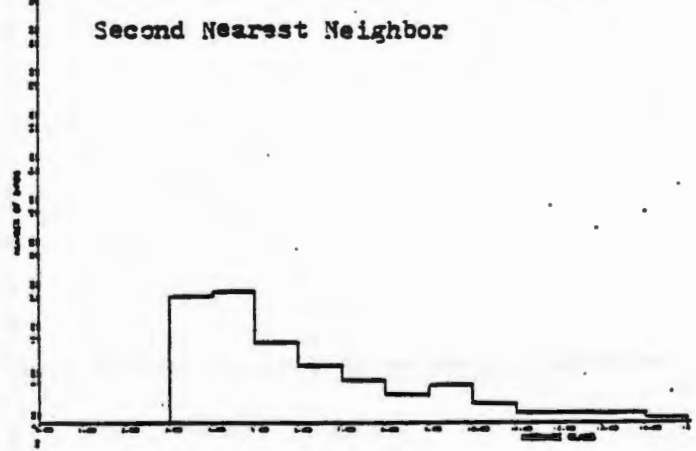
Third Nearest Neighbor
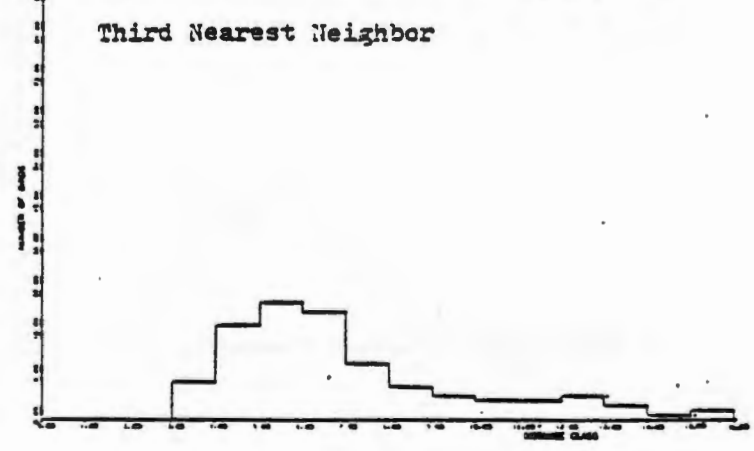
TRIAL 7

First Nearest Neighbor
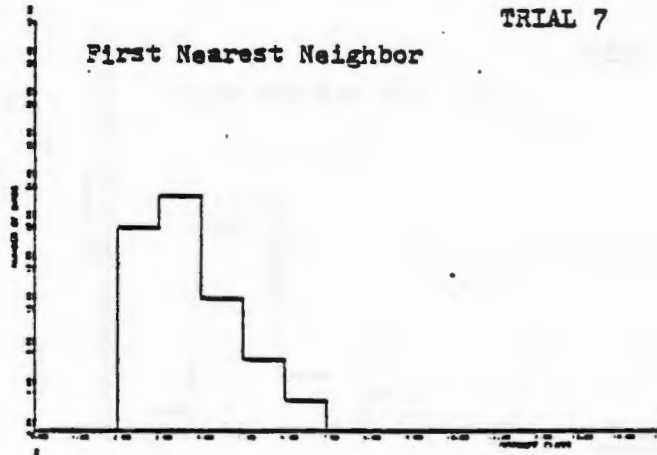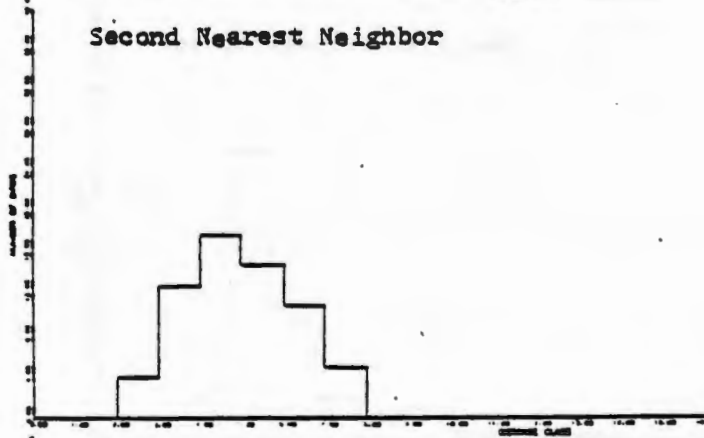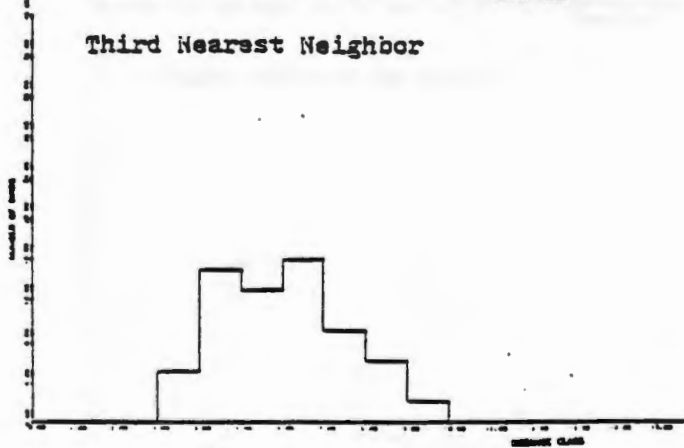
C

Second Nearest Neighbor

Third Nearest Neighbor

TRIAL 8

d

First Nearest Neighbor
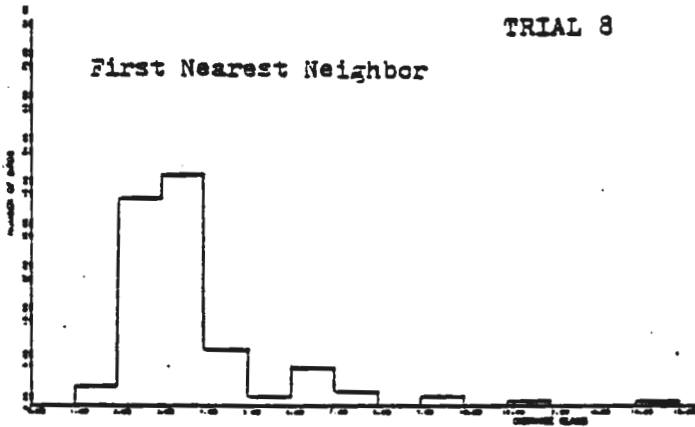
Second Nearest Neighbor
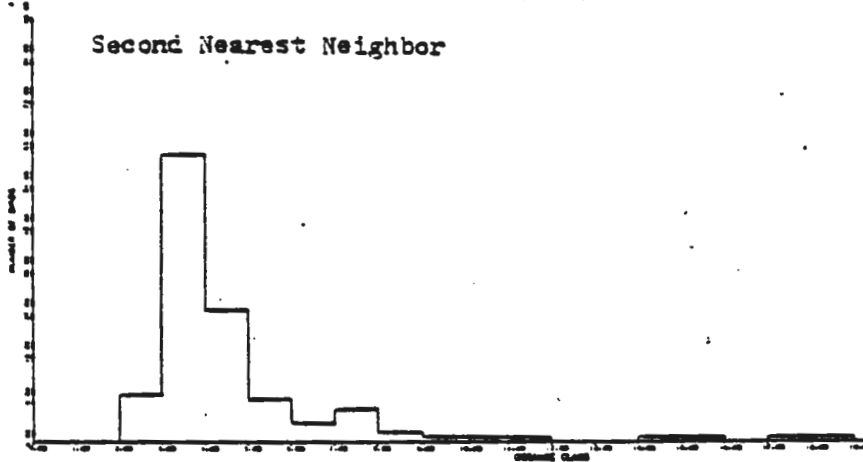
Third Nearest Neighbor
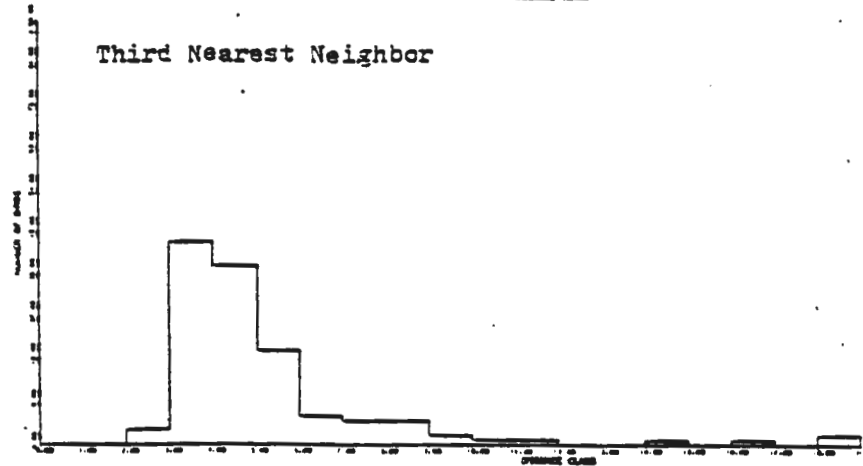
TRIAL 9

First Nearest Neighbor

e
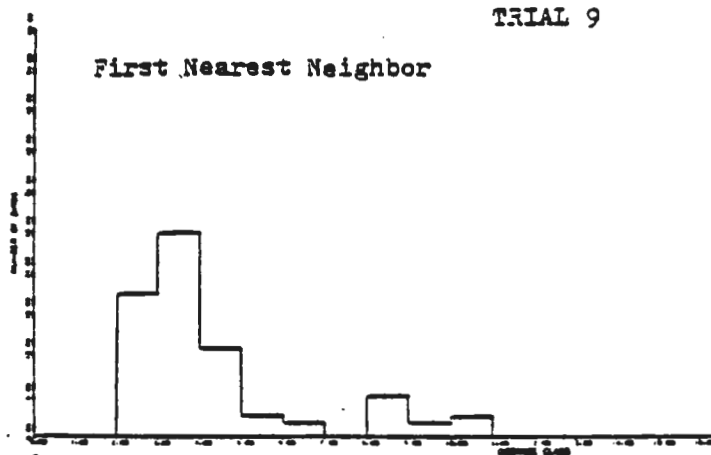
Second Nearest Neighbor
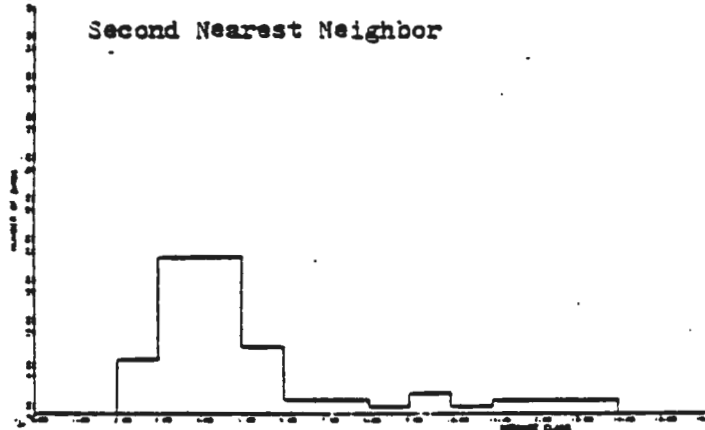
Third Nearest Neighbor
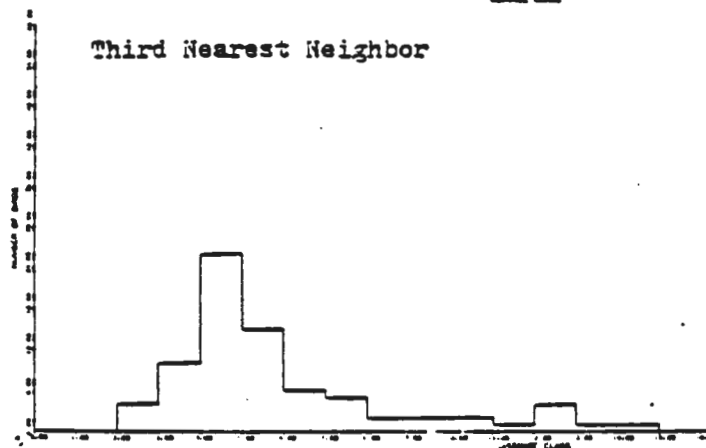
Figure 21. Differences in dominance rank of first
nearest neighbor pairs in the airborne
flocks. Each bird in the flank was
analyzed in turn as the reference bird,
and the difference in dominance rank of
its first nearest neighbor was deter-
mined. This process was done for all
time periods in all trials. The possible
dominance ranks of the reference bird
are listed along the abscissa, with the
mean difference in rank of all identified
nearest neighbors plotted on the ordinate
axis.

MEAN DIFFERENCE IN RANK OF ALL NEAREST NEIGHBORS

DOMINANCE RANK OF REFERENCE BIRD
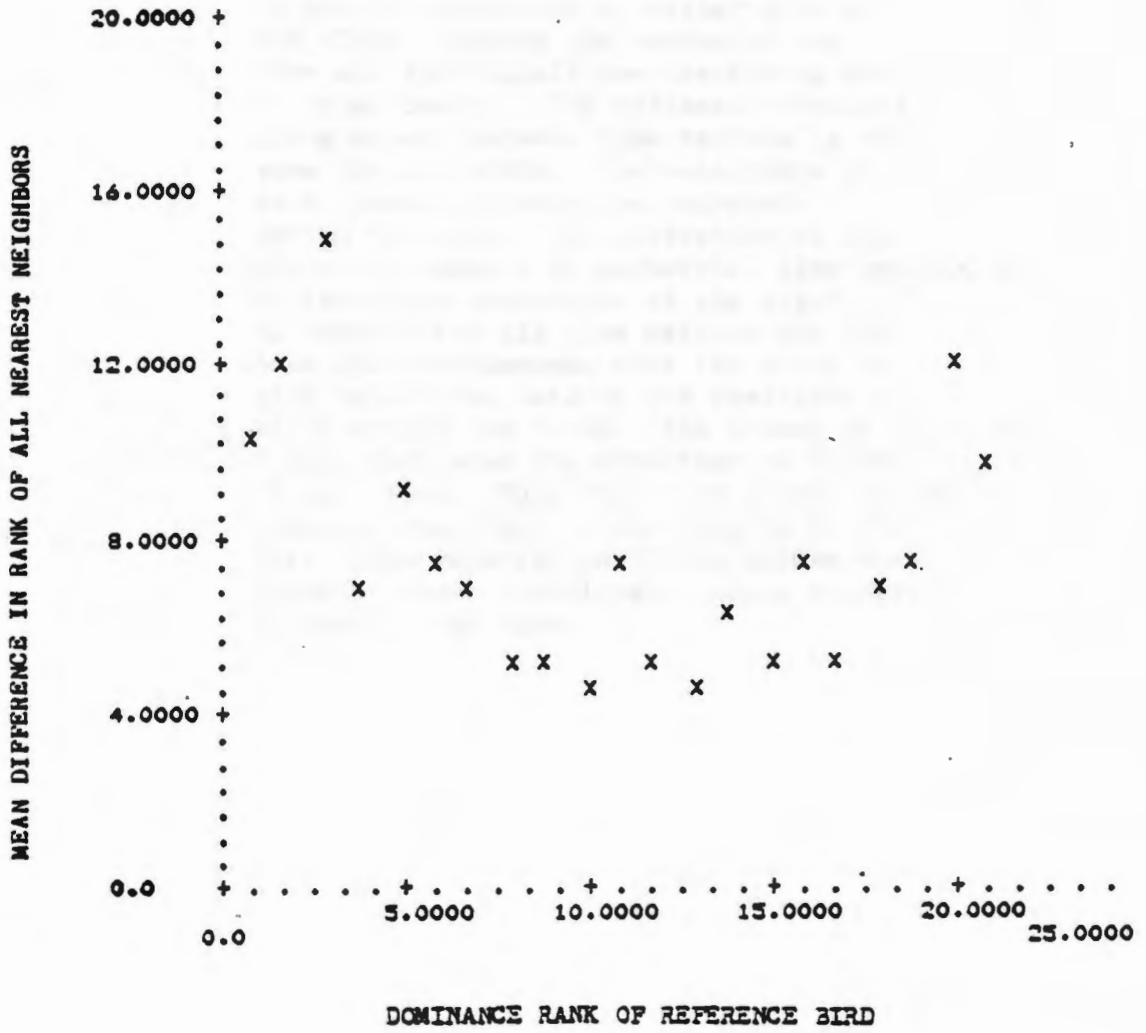
Figure 22.   Flight paths of the central core of a
             flock ( ), with two individuals
             (Δ and 0) travelling to either side of
             the flock. During the course of the
             turn all individuals are describing arcs
             of equal radius. The distance travelled
             along an arc between time periods is the
             same for all birds. The subscripts on
             each symbol indicate the intervals
             during the turn. The alteration of open
             any solid symbols at sequential time periods is
             to faciliate inspection of the figure.
             At each of the six time periods the X-Y
             axes are superimposed over the flock to
             give relational data on the positions of
             birds within the flock. The arrows on the
             X axis indicates the direction of travel
             of the flock. Note that bird starts at the
             right of the flock, while bird is to the
             left. The relative positions within the
             flock of these individuals rotate counter-
             clockwise over time.

time 1

time 2

time 3

time 4

time 5

time 6

TRIAL #1

ASSIGN. NUMBER	REAL IDENT.	DOM. RANK
1	14	6
2	18	7
3	16	10
4	2	2
5	6	19
6	4	3
7	20	21
8	22	20
9	7	9?
10	9	4
11	13	1
12	5	14
13	3	5
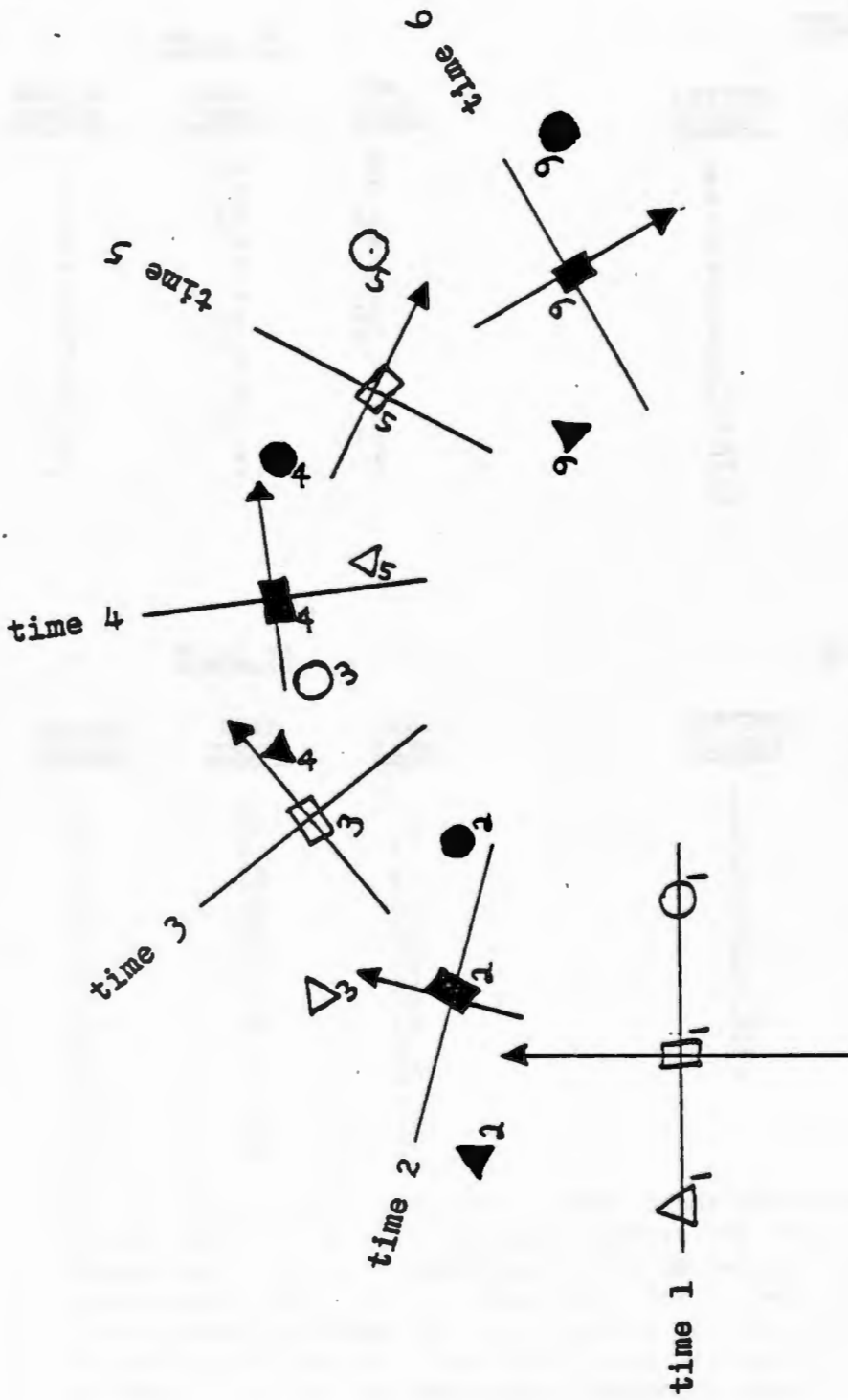
TRIAL #2

ASSIGN. NUMBER	REAL IDENT.	DOM. RANK
1	19	18
2	-	-
3	6	19
4	15	15
5	22	20
6	-	-
7	16	10
8	14	6
9	17	13
10	7	9
11	20	2
12	5	14
13	8	8
14	18	7

TRIAL #6

ASSIGN. NUMBER	REAL IDENT.	DOM. RANK
1	-	-
2	14	19
3	9	4
4	18	8
5	16	5
6	21	15
7	17	21
8	7	13
9	5	17
10	22	18
11	1	3
12	6	20
13	-	-
14	19	16
15	20	7

TRIAL #7

ASSIGN. NUMBER	REAL IDENT.	DOM. RANK
1	-	-
2	8	2
3	14	19
4	19	16
5	20	7
6	7	13
7	16	5
8	4	9
9	21	15
10	17	21
11	5	17

Table 1. Composition os flocks. Three types of information are listed for each trial. Assigned numbers are trial specific levels used only to distinguish birds as unique in the series of photographs for a trial. Identification numbers (ID) were given to each bird and used for the duration of the study to identify specific individuals. Each bird in an airborne flock which could be identified has the associated dominance rank of that individual listed.

TRIAL #8

ASSIGN. NUMBER	REAL IDENT.	DOM. RANK
1	20	7
2	14	19
3	9	4
4	3	11
5	5	17
6	17	21
7	8	2
8	22	18
9	19	16
10	13	6
11	16	5
12	7	13
13	21	15
14	4	9
15	6	20
16	-	-

TRIAL #9

ASSIGN. NUMBER	REAL IDENT.	DOM. RANK
1	17	21
2	14	19
3	6	20
4	16	5
5	20	7
6	5	17
7	1	3
8	2	12
9	15	14
10	18	8
11	22	18
12	21	15
13	4	9
14	13	6
15	19	16
16	-	-

TRIAL #10

ASSIGN. NUMBER	REAL IDENT.	DOM. RANK
1	-	-
2	-	-
3	6	9
4	1	1
5	22	7
6	-	-
7	-	-
8	4	4
9	16	2
10	-	-
11	7	5
12	21	6
13	-	8
14	14	10
15	17	3
16	20	

FRAME # 1

BIRD	X-AXIS (cm)	Y-AXIS(cm)	Z-AXIS (cm)
1	852.7	1399.5	1251.7
2	593.5	1432.9	1335.1
3	385.4	1460.1	1393.9
4	708.2	1131.2	1321.3
5	860.3	1059.3	1378.1
6	873.2	1354.4	1439.8
7	640.8	1344.6	1413.7
8	428.0	1134.1	1395.1
9	567.4	1254.6	1405.0
10	734.6	1170.9	1340.6
11	992.5	1581.7	1457.6

FRAME # 2

BIRD	X-AXIS	Y-AXIS	Z-AXIS
1	1127.5	771.3	1196.2
2	1297.3	911.3	1277.8
3	1119.3	863.7	1298.8
4	1011.5	602.7	1259.6
5	1154.1	607.5	1308.4
6	1165.0	977.0	1427.0
7	1224.9	951.5	1318.1
8	1203.7	651.1	1323.5
9	1245.2	687.1	1270.6
10	1050.6	676.3	1252.4
11	1312.3	1003.7	1402.1

FRAME # 3

BIRD	X-AXIS	Y-AXIS	Z-AXIS
1	1113.3	72.7	1030.5
2	1393.2	228.5	1185.8
3	1049.7	188.4	1155.9
4	1036.2	-24.0	1191.2
5	1223.6	-13.3	1139.0
6	1316.3	323.9	1351.8
7	1046.0	258.5	1229.8
8	1244.8	-1.9	1247.5
9	1160.3	26.2	1048.6
10	1097.2	63.2	1092.7
11	1473.6	315.3	1316.6

Table II. Real-space positions of birds. The displacement
on the X, Y, and Z azes of the Cartesian coordinate
systems defined by the optical axes of the cameras are
listed for each bird in trial seven, for each of the
six points in time at which the flock was photographed.

FRAME # 4

BIRD	X-AXIS	Y-AXIS	Z-AXIS
1	573.0	-567.0	789.8
2	1051.0	-486.1	1003.2
3	592.5	-174.7	961.6
4	601.8	-654.1	1036.5
5	919.4	-716.5	948.5
6	1050.0	-408.3	1178.3
7	780.3	-377.8	1032.7
8	907.4	-713.5	1078.9
9	681.9	-669.5	819.7
10	616.3	-502.9	842.3
11	1165.3	-550.1	1158.3

FRAME # 5

BIRD	X-AXIS	Y-AXIS	Z-AXIS
1	-243.1	-479.2	656.0
2	361.0	-866.5	777.3
3	-145.5	-758.3	781.9
4	490.9	-1029.9	863.6
5	270.6	-1181.9	779.3
6	367.2	-878.4	912.7
7	55.2	-758.0	397.3
8	208.3	-1183.4	878.0
9	-136.2	-1029.4	592.4
10	-140.0	-796.3	725.5
11	492.0	-917.3	949.8

FRAME # 6

BIRD	X-AXIS	Y-AXIS	Z-AXIS
1	-1166.4	-963.6	587.4
2	-424.0	-882.0	598.0
3	-923.5	-841.2	673.2
4	-878.2	-1115.7	684.1
5	-491.9	-1254.8	637.2
6	-452.0	-744.0	679.0
7	-689.4	-608.1	722.2
8	-643.3	-1311.1	683.7
9	-1044.4	-1021.4	408.8
10	-926.1	-505.0	620.7
11	-350.9	-1013.1	800.0

APPENDIX A

Descriptions of birds used in the study. The identification
number of each bird is shown to the left of each description.

BIRD	DESCRIPTION
1	red with white primaries and breast
2	red with black bars and gray belly
3	gray with red nape, light gray primaries and tail
4	dark red with white primaries and tail
5	gray with black bars and tail, white primaries
6	gray with black tail
7	gray with black tail and primaries
8	red and white mottled
9	gray mottled, white nape
10	-----
11	brown with white head
12	black with white nape and breast
13	black with alternating white and black primaries
14	black with white chin and belly
15	black with white nape and back
16	black with white chin, primaries; dark tail
17	black with white chin, primaries, light tail
18	white with black chin and breast
19	white and black mottled
20	white with red chin
21	brown with white primaries
22	black with white primaries; alternating white and black tail

* note with these descriptions, chin refers to the chin and throat.

APPENDIX B

TEST FOR SYNCHRONY OF FILM EXPOSURE BETWEEN CAMERA A AND CAMERA B.

CAMERA A meter reading	ΔT (msec)	CAMERA B meter reading	ΔT (msec)	DIFFERENCE IN METER READING (msec)
0		0		
651	651	650	650	1
1301	650	1299	649	2
1952	651	1950	651	2
2604	652	2602	652	2
3254	650	3253	651	1
3902	648	3903	650	1
4551	649	4554	651	3
5201	650	5204	650	3
5852	651	5855	651	3
6504	652	6505	650	1
7157	653	7157	652	0
7809	652	7809	652	0
8460	651	8459	650	1
9112	653	9111	652	1
9760	650	9760	649	0
10409	649	10410	650	1
11057	648	11059	649	2
11706	649	11709	650	3
12354	648	12358	649	4
13003	649	13008	650	5
13653	650	13657	649	4
14303	650	14307	650	4
14954	651	14957	650	3
15604	650	15608	651	4
16253	649	16258	650	5
16904	651	16907	649	3
17556	652	17556	649	0
18208	652	18206	650	2
18859	651	18855	649	4
19508	649	19507	652	1
20159	651	20158	651	1
20808	650	20808	650	0
21495	651	21458	650	1
22111	652	22109	651	2
22761	650	22760	651	1
23410	649	23412	652	2
	AVG = 650.39		AVG = 650.34	
	STD = 1.35		STD = 1.01	

APPENDIX C

DISTANCES AND ANGULAR RELATIONSHIPS BETWEEN BIRDS IN MODEL FLOCK

actual measured distance between bird pairs...... 121.92cm

actual measured angle between birds....... 30.0 degrees

FRAME #1

BIRD PAIR	DISTANCE
1-2	116.53cm
1-4	126.21cm
3-2	122.35cm
3-4	124.58cm
5-6	112.59cm
5-8	125.65cm
7-6	126.18cm
7-8	117.63cm

AVG 121.46
STD   5.22
VAR 27.25

4.0% ERROR

FRAME #2

BIRD PAIR	DISTANCE
1-2	115.54cm
1-4	124.28cm
3-2	123.97cm
3-4	110.34cm
5-6	116.25cm
5-8	124.26cm
7-6	118.95cm
7-8	113.49cm

AVG 118.39
STD   5.48
VAR 30.03

2.9% ERROR

FRAME #3

BIRD PAIR	DISTANCE
1-2	126.72cm
1-4	127.93cm
3-2	123.95cm
3-4	121.20cm
5-6	127.45cm
5-8	124.28cm
7-6	126.11cm
7-8	127.94cm

AVG 125.70
STD   2.39
VAR   5.71

3.1% ERROR

FRAME #4

BIRD PAIR	DISTANCE
1-2	129.72cm
1-4	115.42cm
3-2	122.22cm
3-4	122.12cm
5-6	128.47cm
5-8	113.56cm
7-6	114.58cm
7-8	124.86cm

AVG 120.67
STD   6.48
VAR 41.99

1.0% ERROR

FRAME #5

BIRD PAIR	DISTANCE
1-2	133.75cm
1-4	117.35cm
3-2	107.19cm
3-4	121.87cm
5-6	126.62cm
5-8	129.56cm
7-6	106.07cm
7-8	115.54cm

AVG 119.74
STD 10.08
VAR 101.60

1.8% ERROR

ALL FRAMES

BIRD PAIR	AVERAGE DISTANCE	STD	ANGLE	STD
1-2	124.48cm	7.24	28.3	2.10
1-4	122.25cm	4.95	32.7	1.34
3-2	118.85cm	6.45	33.1	1.27
3-4	117.47cm	5.23	27.2	1.77
5-6	122.27cm	6.55	34.1	2.21
5-8	123.47cm	5.33	30.6	1.84
7-6	118.39cm	7.57	28.3	2.32
7-8	119.89cm	5.56	29.2	1.08

APPENDIX D

Distances between birds at the six time periods (Frames) in trial
seven. Mean separation distance, and the mean distance to first
nearest neighbor are shown for each time period. Identification
numbers of birds forming nearest neighbor pairs, and associated
distances, are also listed.

FRAME # 1

MEAN SEPARATION DISTANCE= 303.6CM
   AVERAGE DISTANCE TO NEAREST
   NEIGHBOR= 115.8 (STD= 46.1)

BIRD	NEAREST NEIGHBOUR	SEPARATION DISTANCE(cm)
1	3	166.6
2	3	123.1
3	2	121.3
4	10	91.5
5	4	142.9
6	2	121.4
7	10	210.7
8	9	81.4
9	8	61.4
10	4	51.5
11	6	121.8

FRAME # 2

MEAN SEPARATION DISTANCE= 767.3
   AVERAGE DISTANCE TO NEAREST
   NEIGHBOR= 96.5 (STD= 27.5

BIRD	NEAREST NEIGHBOR	SEPARATION DISTANCE(cm)
1	10	139.0
2	7	95.3
3	7	110.7
4	10	63.6
5	8	66.1
6	11	132.6
7	3	85.3
8	3	96.3
9	4	76.2
10	4	33.6
11	6	132.6

FRAME # 3

MEAN SEPARATION DISTANCE= 424.3CM
   AVERAGE DISTANCE TO NEAREST
   NEIGHBOR= 116.5 (STD= 42.1)

BIRD	NEAREST NEIGHBOR	SEPARATION DISTANCE(cm)
1	10	65.0
2	1	176.7
3	7	101.9
4	10	145.0
5	8	111.1
6	11	166.3
7	3	101.9
8	3	111.1
9	1	83.3
10	1	65.0
11	6	166.3

FRAME # 4

MEAN SEPARATION DISTANCE= 380.1
   AVERAGE DISTANCE TO NEAREST
   NEIGHBOR= 173.6 (STD= 60.4

BIRD	NEAREST NEIGHBOR	SEPARATION DISTANCE(cm)
1	10	92.6
2	9	191.6
3	9	260.1
4	9	231.5
5	8	130.7
6	11	184.4
7	3	260.1
8	5	130.7
9	1	151.1
10	1	92.6
11	6	184.3

FRAME # 5   FRAME # 6

MEAN SEPARATION DISTANCE= 405.0CM   MEAN SEPARATION DISTANCE= 429.
 AVERAGE DISTANCE TO NEAREST   AVERAGE DISTANCE TO NEAREST
 NEIGHBOR= 141.4 (STD= 62.8)   NEIGHBOR= 163.6 (STD= 60.

BIRD	NEAREST NEIGHBOR	SEPARATION DISTANCE(cm)		BIRD	NEAREST NEIGHBOR	SEPARATION DISTANCE(cm)
1	9	159.7		1	9	223.9
2	9	134.5		2	9	109.9
3	10	98.1		3	10	84.7
4	1	273.3		4	1	224.2
5	4	116.7		5	8	168.1
6	7	112.8		6	7	105.9
7	11	429.4		7	2	241.1
8	4	116.7		8	8	168.1
9	1	159.7		9	1	223.8
10	3	98.1		10	3	82.7
11	6	112.8		11	6	172.1

APPENDIX E

Headings in the horizontal and vertical planes of the flock, and of all birds in the flock. Distance travelled and heading maintained by birds between each pair of sequential time frames in the series of photographs in trial seven are shown. The mean heading of all birds (flock heading) and associated standard deviation (STD) are listed.

HORIZONTAL PLANE DISPLACEMENT

7/25/80

TRIAL # 7

FRAME 1 TO FRAME 2

FLOCK HEADING= 300.20 STD= 6.15

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	688.8 CM	293.62	6.58
2	649.4 CM	298.01	2.19
3	666.1 CM	290.78	9.42
4	612.4 CM	299.85	0.35
5	544.5 CM	303.21	3.01
6	656.8 CM	297.99	2.22
7	745.6 CM	322.21	22.00
8	604.3 CM	297.36	2.85
9	646.0 CM	296.08	4.12
10	593.5 CM	302.57	2.37
11	662.9 CM	298.97	1.23

FRAME 2 TO FRAME 3

FLOCK HEADING= 271.80 STD= 5.08

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	716.0 CM	268.83	2.96
2	696.1 CM	277.99	6.19
3	693.7 CM	264.12	7.68
4	630.9 CM	272.26	0.46
5	647.0 CM	276.21	4.41
6	670.4 CM	281.36	9.57
7	663.5 CM	254.27	17.53
8	658.7 CM	273.60	1.80
9	702.3 CM	262.68	9.12
10	635.2 CM	274.35	2.55
11	713.3 CM	283.57	11.77

FRAME   3 TO FRAME   4

FLOCK HEADING= 239.34   STD=   5.22

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	872.7 CM	229.91	9.44
2	812.8 CM	244.45	5.10
3	615.3 CM	218.46	20.89
4	784.0 CM	235.59	3.76
5	789.5 CM	246.61	7.26
6	798.2 CM	250.01	10.67
7	739.0 CM	241.48	2.14
8	805.4 CM	244.63	5.29
9	874.8 CM	235.49	3.86
10	787.4 CM	229.30	10.05
11	933.8 CM	250.12	10.78

FRAME   4 TO FRAME   5

FLOCK HEADING= 209.84   STD=   2.91

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	902.1 CM	203.81	6.03
2	820.2 CM	208.85	0.99
3	956.6 CM	218.43	8.60
4	810.2 CM	208.02	1.81
5	816.2 CM	215.66	5.82
6	854.9 CM	215.34	5.51
7	772.1 CM	210.53	0.70
8	865.9 CM	213.91	4.07
9	522.2 CM	203.74	6.09
10	820.4 CM	201.23	8.61
11	800.2 CM	208.38	1.46

FRAME   5 TO FRAME   6

FLOCK HEADING= 185.02   STD=   1.60

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	926.5 CM	182.13	2.89
2	806.0 CM	181.19	3.84
3	792.2 CM	186.03	1.00
4	806.2 CM	186.27	1.24
5	779.1 CM	185.46	0.44
6	874.3 CM	184.47	0.56
7	772.7 CM	188.36	3.34
8	882.8 CM	188.53	3.51
9	926.6 CM	179.50	5.53
10	793.9 CM	187.90	2.97
11	855.6 CM	186.53	1.50

VERTICAL PLANE DISPLACEMENT

7/25/80

TRIAL # 7

FRAME 1 TO FRAME 2

FLOCK HEADING= 353.04   STD= 1.32

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	688.8 CM	354.54	1.51
2	649.4 CM	354.94	1.90
3	666.1 CM	351.79	1.25
4	612.4 CM	354.22	1.18
5	544.5 CM	352.65	0.39
6	656.8 CM	354.51	1.48
7	745.6 CM	352.63	0.41
8	604.3 CM	353.20	0.16
9	646.0 CM	347.99	5.04
10	593.5 CM	351.45	1.58
11	662.9 CM	355.20	2.17

FRAME 2 TO FRAME 3

FLOCK HEADING= 349.64   STD= 1.72

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	716.0 CM	347.43	2.21
2	696.1 CM	352.40	2.76
3	693.7 CM	348.11	1.53
4	630.9 CM	353.77	4.13
5	647.0 CM	344.82	4.83
6	670.4 CM	353.56	3.92
7	663.5 CM	352.35	2.71
8	658.7 CM	353.37	3.73
9	702.3 CM	341.57	8.07
10	635.2 CM	345.44	4.20
11	713.3 CM	353.11	3.47

FRAME 3 TO FRAME 4

FLOCK HEADING= 346.29 STD= 1.54

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	872.7 CM	343.99	2.30
2	812.8 CM	347.02	0.73
3	615.3 CM	341.59	4.69
4	784.0 CM	348.63	2.34
5	789.5 CM	346.04	0.25
6	798.2 CM	347.45	1.16
7	739.0 CM	348.52	2.23
8	805.4 CM	347.90	1.61
9	874.8 CM	344.83	1.46
10	787.4 CM	341.50	4.79
11	933.8 CM	350.24	3.95

FRAME 4 TO FRAME 5

FLOCK HEADING= 347.09 STD= 1.72

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	902.1 CM	351.47	4.38
2	820.2 CM	344.01	3.08
3	956.6 CM	349.17	2.08
4	810.2 CM	347.67	0.58
5	816.2 CM	348.03	0.94
6	854.9 CM	341.90	5.19
7	772.1 CM	346.11	0.99
8	865.9 CM	346.60	0.49
9	922.2 CM	345.73	1.36
10	820.4 CM	351.78	4.69
11	800.2 CM	344.90	2.19

FRAME 5 TO FRAME 6

FLOCK HEADING= 349.25 STD= 1.84

BIRD	DISPLACEMENT IN 3-SPACE	HEADING	ANGULAR DEVIATION
1	926.5 CM	355.76	6.51
2	806.0 CM	347.15	2.10
3	792.2 CM	352.11	2.86
4	806.2 CM	347.14	2.11
5	779.1 CM	349.49	0.24
6	874.3 CM	344.54	4.71
7	772.7 CM	346.90	2.35
8	882.8 CM	347.29	1.96
9	926.6 CM	348.57	0.68
10	793.9 CM	352.41	3.16
11	855.6 CM	349.91	0.66

APPENDIX F

Dominance matrices for the three time periods during which the
flocks were photographed. Each matrix consists of data from
six 90 minutes observation sessions. The ratio of the number of wins to
the number of losses that each bird had as a result of its interactions
with other flock members was used to establish dominant and subordinate
birds in the airborne flocks.

JUNE 8 - JUNE 21

LOSSES

BIRD (WINS)	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	# wins	Ratio (w/l)
01		1			1		1	3	2		4	1	1			1		2	3		3	2	25	0.89
02			2		6	3	3		2		1			2	2	3		1				6	31	0.86
03	2	1		1	3	1	3	6			1			1		1			1	2		2	25	1.49
04		2	2		3	1	1	1				2			2				1	1	1	1	18	2.25
05	2				2	1					6	1	1		1	2	1		1		2	2	22	0.81
06			2												·		1		1		2		06	0.33
07			1	1	5	2		2	1										2		1		15	1.15
08	3	2	5		2	3						1	1	2		1	1	2	2			3	28	1.17
09		1	2				1	1			2			3	1		3	2	3	1	2	5	27	1.80
10																								
11	3				2		1					2				2					2	1	13	0.68
12							1										1		1			3	06	0.60
13	5	8			2	1.		4	1					7	6			5	4	2	1	11	59	8.43
14	1	12	3		1		1	3	1		1		1			1		3	2		1	1	32	1.43
15	4	1		1				1	1		1			1		1			1		2	1	15	0.75
16	2				3			1						1	1						1	1	10	0.72
17		1	1		1									2					1	2		1	09	0.82
18		5	1		2			1			1			2					2		1	3	18	1.20
19	1	1					1	1	1		1	1	2	4	1							2	14	0.56
20	4			1	2			2			1	1			1	1	1					5	19	2.37
21	1																						01	0.05
22		1		2			1		3		1	1	2	1	1	1							14	0.28
# loss	28	36	17	08	27	18	13	24	15		19	10	07	23	20	12	11	15	25	08	19	50	407 TOTAL	

JUNE 23 – JULY 10

LOSSES

BIRD	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	# wins	Ratio (w/l)
01			2	2	1		2		1		7	1	1	2	3	1	1	4	1	2	2	2	35	3.18
02				1	1	1		1			1		1	6	2	4	2		2		1	3	26	0.89
03	2		1		4	2	2				2	1			1		3	1		1	1	3	24	1.26
04			1		2						2	1			1			1				1	09	0.60
05		1	1		2	2					2	1	3		1			2				2	17	0.65
06			4													1			1		1	3	10	0.48
07						1		2						1	2		1		1			1	09	0.60
08	1	1	9	5	5	3	1		1		9	4	1			2	2	5	3	1		4	66	4.70
09					1			1			1					1			1			2	07	0.58
10																								
11	1				1	1						2			1	1				1	1	2	11	0.32
12		1																1		2			04	0.28
13		2		1	8			1	5		2			2	6			2	4	1	1	2	37	2.47
14		9	1		2	1								2	1	1						2	19	0.91
15		2	1	2	3	1	4							2			7			1		2	25	0.89
16	1	2				1		1	3			1			1	2			1	1	2	4	23	1.79
17	3			1	1	1		1			1			2	1				1		2		14	0.50
18	1	3		1	1						3	1	1		2	2	2			2		2	21	0.88
19		1						1				1	2		1		1		1				08	0.38
20	1	7		2	2	2	2	4	1		2	1	6	5	2		4	4	6		2	2	55	4.23
21	1					1		1			1						1						05	0.31
22							1				1				1		3	3	1				10	0.27
# loss	11	29	19	15	26	21	15	14	12		34	14	15	21	28	13	28	24	21	13	16	37	435	

TOTAL

JULY 14 - JULY 26

LOSSES

BIRD	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	# wins	Ratio (w/l)
01		1		5	2	1	2	4	2		3		1	1	3	2		2		1	5	3	38	2.00
02	1		1	1	2	3	3		1		2	2		5	3	3	2	3		1	1	2	36	0.89
03		3		1		3		2	4				2	2	2	2		1		1		1	24	0.92
04		1	4					3			2			3		5	2	3		1	1	1	26	1.00
05		4	1			2	2	1	2			1			4	4	1	1	1			1	25	0.49
06	1	1	2				2		1						2			1				4	14	0.31
07		1		1		6		3			2		1	1			2		1		1		19	0.73
08	1	4	1	4	10	3	2		5		8	3		1	2	7	2	3	1		4	1	62	2.10
09			3	2	2	7	3	3			3	3	6	2	4	1	8	4		1		4	56	2.00
10																								
11		2	4	1	5	1	1	3				4			2			2	6	1		3	35	0.95
12		2	2	2	11	5	2	2	2		1		5	2	1	4	2	1	2	3	1		50	2.78
13	1	3	2	1	5	2			4		3	1		1	3		1	4	3	2		1	37	1.68
14		5		1							1			1	2			2	1			1	13	0.43
15	3	1		1	1	2	1	4			1		1				8	1	1			1	26	0.70
16	3	4	3	3	5	4	3	2	1		4	2	7	5	3		3		2	4	5	2	65	1.91
17	3	2					2		.		1							1		1	1	1	11	0.30
18	1	2	2	4	2	2	1		1		3		4	3	1		1		3	2		2	34	1.03
19	1	2		1		1					2			1	1					3	1	1	14	0.58
20	3	2		1	2	1	1	2	1			1		2	4	3	1					3	27	1.59
21		1	1		1	2	1	1			1	1			4				1				14	0.64
22	1			1	1	2					1	1			1			2	5				15	0.45
# loss	19	41	26	26	51	45	26	29	28		37	19	22	30	37	34	37	33	24	17	22	33	641 TOTAL	