

5

Three-dimensional structure and dynamics of bird flocks

FRANK HEPPNER

5.1 Introduction

Of all coordinated groups of moving vertebrates, birds are at the same time the easiest to observe and perhaps the most difficult to study. While fish can be brought into a laboratory for study, and many mammals move in a two-dimensional plane, a single bird in an organized flock can move through six degrees of freedom at velocities up to 150 km/hr. Present three-dimensional analysis techniques generally demand either fixed camera or detector positions, so free-flying flocks must either be induced to fly in the field of the cameras, or the cameras must be placed in locations where there is a reasonable probability that adventitious flocks will move through the field. Perhaps because it has been so difficult to obtain data from free-flying natural flocks, there is now a current of imaginative speculation, and lively controversy, in the literature on flock structure and internal dynamics.

Birds can fly in disorganized groups, such as gulls orbiting over a landfill, or organized groups, such as the Vs of waterfowl (Fig. 5.1a). To the evolutionist, behaviorist, or ecologist, *any* group is of interest, but I will primarily consider only the organized groups. Heppner (1974) defined organized groups of flying birds as characterized by coordination in one or more of the following flight parameters: turning, spacing, timing of takeoff and landing, and individual flight speed and direction. The term used for such organized groups was "flight flock," but for consistency in this volume, the term "congregation" will be used herein.

Two general questions have driven the examination of bird congregations. The first, usually expressed while observing a skein of geese flying overhead, is, "Why do they fly in this precise alignment?" The second is prompted by the sight of perhaps 5000 European Starlings, *Sturnus vulgaris*, turning and wheeling over a roost. "How do they manage to achieve such coordination and polarity?" The first question is usually asked in reference to relatively large birds, like waterfowl, flying in *line formations* (Heppner 1974; Fig. 5.1a): groups of birds



(a)



(b)

Figure 5.1. (a) A V-formation of Canada Geese (i.e. line formation). Notice, in this oblique two-dimensional view, the difficulty of determining distance between birds and angular relationships between birds. (b) A cluster formation of mixed blackbirds.

flying in a single line, or joined single lines. Typically, such formations are approximately two-dimensional, the birds all lying in an X-Y plane parallel to the ground. The “how” question is customarily asked about relatively large flocks of small birds, like sandpipers, flying in *cluster formations* (Fig. 5.1b): flocks characterized by development in the third dimension, and rapid, apparently synchronous turns.

Attempts at analysis of structure and dynamics in these two major classes of organized flight formations have been driven both by the characteristics of the formations and the types of questions that have been asked. In the line formations, the functional significance (i.e. why) of the groupings has been of cardinal interest; therefore data have been sought on the values of parameters that might be supportive of hypotheses concerning costs and benefits to the individual. Because these formations have characteristically been interpreted as two-dimensional, structural analysis, although challenging due to the ephemeral nature of flocks, has not required true three-dimensional analysis techniques. In contrast, it is the synchronous and coordinated turning of the cluster flocks that has drawn the greatest interest. Questions such as, “Is there a leader in such groups?” or “If there is no leader, how is coordination achieved?” have spurred the structural analyses. However, because these formations occupy a three-dimensional volume, the formidable technical challenges involved have produced few field studies to date.

In this chapter, I will explore how progress in the study of both line and cluster flocks has proceeded in stepwise fashion, sometimes being stimulated by a new technique, at other times prompted by a testable (as opposed to speculative) idea.

5.2 Line formations

5.2.1 Theoretical considerations

Speculation and unsupported conclusions about the function of apparent structure in line formations have a long history. Rackham (1933) translated Pliny’s authoritative observation in the first century A.D. that geese “travel in a pointed formation like fast galleys, so cleaving the air more easily than if they drove at it with a straight front; while in the rear the flight stretches out in a gradually widening wedge, and presents a broad surface to the drive of a following breeze.” Two thousand years later, Franzisket (1951) posited that close-formation flight provided an area of turbulence-free air. In contrast, Hochbaum (1955), attempting to explain why waterfowl fly in staggered formation, hypothesized that it was to “avoid the slipstream of rough air produced by the movement of its companions.” Hunters often offer the folk suggestion that birds in these formations might be “drafting,” like auto or bicycle racers do: tucking in behind the vehicle

ahead to reduce air resistance. Geyr von Schweppenburg (1952) suggested that a phase relationship in wing beating might be important in the aerodynamics of flight in line formations. Nachtigall (1970) found such a relationship in geese, but von Berger (1972) and Gould (1972) did not. Hainsworth (1988) did not see phase synchrony in pelicans. If the wings of each bird in a flock are regarded as independent oscillators, there will be some periods of time in which significant numbers of the flock will be in temporary synchrony, and this may have been what Nachtigall observed.

Non-aerodynamic hypotheses also have been offered for line formation flight. One of the most compelling suggestions stated that structured formations facilitate the collection of information by and from flock mates (see Dill, Holling & Palmer, Ch. 14 for a discussion of this possibility in fish schools). Hamilton (1967) suggested that a stagger formation allowed communication between individuals. Forbush et al. (1912) and Bent (1925) suggested that staggered flight permitted a clear field of vision to the front, while at the same time allowing a leader to fly at the head of the formation. Heppner (1974), Molodovsky (1979), and Heppner et al. (1985) all offered the possibility that V or echelon flight lines might be the result of the optical characteristics of the birds' eyes.

Until 1970, students of line formations could only offer streams of hypotheses about function, because there was no suggestion about what parameter(s) might be useful to measure to test those hypotheses. However, Lissaman and Shollenberger (1970) published a seminal, but enigmatic, paper that suggested the function of the V-formation was to enable each bird in line to recapture energy lost by the wingtip vortex produced by the preceding bird. According to their hypothesis, birds abreast in line, flying tip-to-tip, should have a range approximately 70% greater than a lone bird. Distance between wingtips was inversely proportional to maximal energy recapture. In other words, the closer neighbors are, the higher the potential energy savings. Based on Munk's (1933) stagger-wing theory from aircraft aerodynamics, they predicted that the "optimal" V-formation formation (Fig. 5.2) was achieved at a tip spacing equal to 1/4 of the wingspan. However, the Lissaman and Shollenberger (1970) paper was vague; it presented neither the theoretical equations nor sample calculations illustrating their predicted energy savings. Furthermore, there were some major deviations from biological reality. For instance, flapping flight (as opposed to gliding aircraft flight) was not considered. May (1979), in a brief review of flight formation, suggested that Lissaman and Shollenberger's (1970) calculations predict an optimal V angle for saving energy of roughly 120 degrees.

Hummel (1973, 1983) also felt that significant power savings were possible by V-formation flight and presented the calculations he used to arrive at this conclusion. He argued that the power reduction for a V-formation flock as a whole

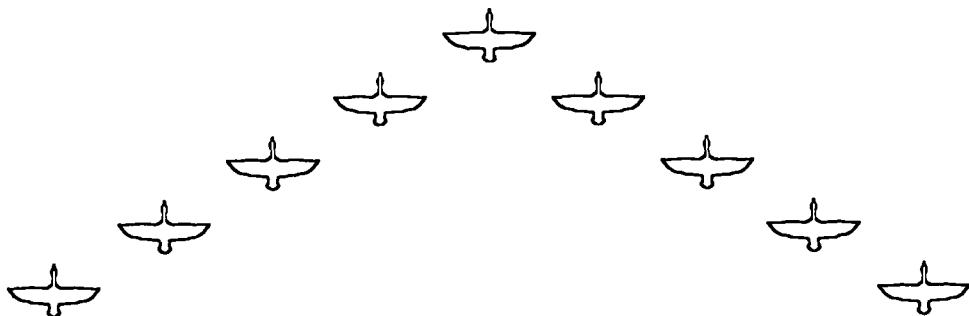


Figure 5.2. An optimal V-formation (Lissaman & Shollenberger 1970).

was strongly dependent on the lateral distance between wingtips, whereas energy savings for individuals in a flock could be affected by longitudinal distances between wingtips. Haffner (1977) attempted to replicate Lissaman and Shollenberger's predicted energy savings also using Munk's stagger theorem, and only obtained a calculated 22% potential energy saving for formation flight. When Haffner then modified the calculation using Cone's (1968) flapping wing theory, the potential maximum energy saving dropped to 12%. Several investigators seized this possibility of a testable hypothesis: determine the geometry of a flock and the distance between the birds, and then the tip-vortex hypothesis could be tested. There was now incentive to develop analytic techniques for the spatial structure of line formations.

5.2.2 Data collection

If a photograph of a level V-formation of geese was taken when the birds were directly over the camera position (or if the camera was directly over the birds), there would be little problem in determining either the geometric relationship of the birds in the formation or the distances between two birds. A known distance, say bill-to-tail length, could be used to establish a distance scale. However, the number of times line-flying birds fly directly over an observer in the field is sufficiently small to tax the patience of the most dedicated researcher. Heppner (1978) made a fruitless attempt to fly a radio-controlled, camera-equipped model airplane directly over goose flocks, but the geese were faster than the aircraft.

If a photograph is taken at an oblique angle to an oncoming or departing V-formation (Fig. 5.3), perspective will change both the angle between the legs of the V and the distances between birds. Gould and Heppner (1974) published the first technique for determining the angular relationship and distances between Canada Geese, *Branta canadensis*, flying in a V. Their technique employed a single cine camera and assumed that (1) the birds were flying in a level plane, (2)

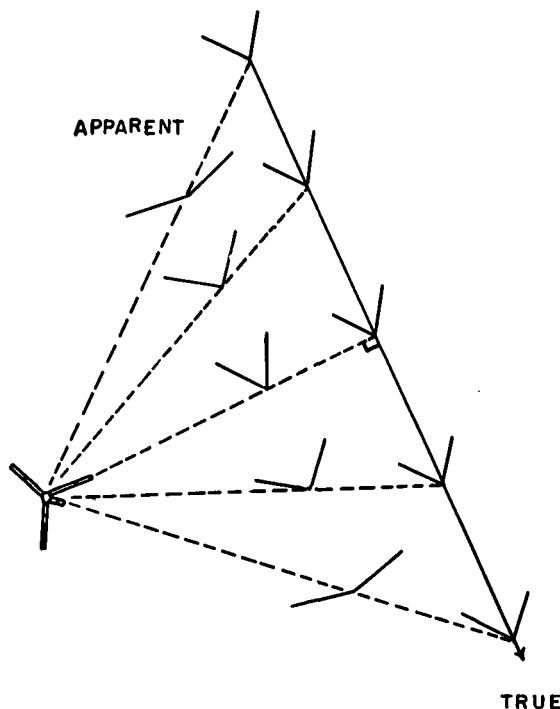


Figure 5.3. Overhead view, looking down at a camera mounted on a tripod, tracking a V-formation that maintains a constant angle between the legs during its passage. The apparent angle of the V, as seen through the viewfinder and recorded on the film, changes as the birds approach their nearest point to the camera and then depart. At the point of closest approach, the apparent angle is at a minimum, and a line drawn between the camera position and the head of the formation at closest approach describes a right angle with the flight path. This angular relationship is then used for projective geometry to calculate the true angle (from Gould & Heppner 1974).

the flight path was a straight line, and (3) the shape of the formation did not substantially change in the few seconds needed for filming. The key observation for this technique (Fig. 5.4) was that when the formation was at its closest point to the camera position, the apparent angle of the legs of the V on the film was at a minimum, while the angle of the optical axis of the camera above the horizon was at a maximum. By marking the angular elevation of the camera at this point of closest approach, it was possible to use projective geometry (Slaby 1966) to obtain the true angle of the formation and the distances between birds. In the five formations they measured, the true V angle was 34.2 ± 6.4 degrees, and the distance between the centers of the birds was 4.1 ± 0.8 m.

O'Malley and Evans (1982) used this technique to measure the angle of the V-formation in White Pelican, *Pelecanus erythrorhynchos*, flocks, and found a mean angle of 69.4 ± 4.5 degrees. They noted that the range of their values was

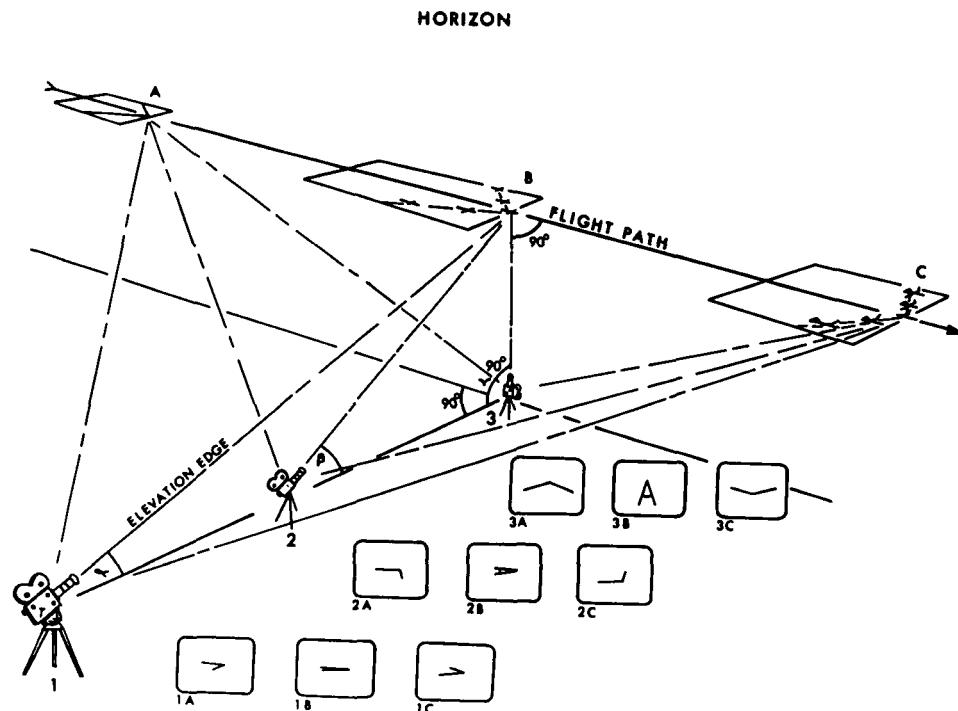


Figure 5.4. Relationship of camera position to flight path, apparent angle in the viewfinder, and camera elevation in a V-formation. This relationship forms the basis for the projective technique used to calculate true angle and distance between birds. (From Gould & Heppner 1974).

large (24–122 degrees) and did not seem to follow a pattern in flight direction, formation type, or flight size. Hainsworth (1988) filmed echelon formations of Brown Pelicans, *Pelecanus occidentalis*, that flew directly overhead, then in a straight line away from the camera. A known distance, the outstretched wing-spread of a pelican, was used as a scale to determine wingtip-to-wingtip spacing which ranged from –171 cm (overlap) to +183 cm.

Williams et al. (1976) used a mobile, modified small boat radar called an “ornithar” to determine the angle between the legs of a V-formation of Canada Geese. The portable radar technique offered smaller distortion due to perspective than optical methods, approximately 3 degrees maximum, but individual birds were not resolvable. V angles ranged from 38 to 124 degrees. Interestingly, there was greater variance among formations than within the same formation over time. In 1975, Heppner, using Gould and Heppner’s (1974) optical method, and Williams et al. (1976), using their radar method, both measured the same formations at the same time at Iroquois National Wildlife Refuge in New York. Two formations met the requirements for measurement for both techniques, i.e. they

were large enough for radar and well-organized enough at the apex for optical measurements. Both methods yielded essentially identical results (Williams et al. 1976).

Although it has not yet been used for looking at flocks, a technique developed by Pennycuick (1982), and described in detail by Tucker (1988, 1995), offers potential for following flight paths of individual birds. It makes use of a device called an "ornithodolite," an optical range finder with a 1-m base mounted on a panoramic head that electrically records elevation and azimuth, with the range indicated by the range finder. In this way, a continuous record of a bird's three-dimensional flight path was obtained. Error in the system increased with distance of the bird from the instrument. At a range of 1 km the true position of the bird is somewhere within a 10 m³ "volume of uncertainty." Tucker (1991) used this technique to follow the flight paths of landing vultures. One could, presumably, use a modification of this technique for tracking individual birds in a flock, but one would need either one ornithodolite for each bird, or a combination of ornithodolites and some accessory system for tracking the flock, such as the portable radar or optical techniques already described.

Tracking radars (as opposed to planned-position indicator radars, like the familiar airport screen) have been used to follow individual birds. There is no technical reason why the technology that has been developed to track multiple targets for military purposes could not be used for bird flocks. However, as Vaughn (1985) pointed out in his excellent review of birds and insects as radar targets, high cost and limited accessibility to high-precision radar tracking devices have reduced the number of active radar ornithologists to a handful. However, there are several excellent studies on tracking of individual birds from the 1970s (DeMong & Emlen 1978; Emlen 1974; Vaughn 1974) that indicated the potential of the technique.

If there is such a thing as a key paper in line formation flight in birds, it is probably Lissaman and Shollenberger (1970). They proposed, for the first time, a *testable* hypothesis about flock formation. Although the Lissaman and Shollenberger paper has had a powerful effect on stimulating thought and action, there has never been a direct experimental test of the aerodynamic assumptions in the paper. Haffner's (1977) unpublished study of Budgerigars, *Melopsittacus undulatus*, flying in a wind tunnel with smoke plumes suggested that the tip vortex in flapping flight was interrupted during the wingstroke cycle. Both Rayner et al. (1986) and Spedding (1987) found that tip vortices behind flying animals moved both vertically and horizontally during the wingstroke, making precise positioning relative to neighbors less advantageous. Most investigators of the structure of the V-formation have found wide variation in spacing and angular positions (Hainsworth 1988; O'Malley & Evans 1982), but have interpreted this variation

as a failure of birds to maximize energy savings, rather than rejecting Lissaman and Shollenberger's (1970) energy-saving model.

5.3 Cluster formations

5.3.1 Function and synchrony

The phenomenon of coordinated flight has been known since the ancients. The redoubtable Pliny (Rackham 1933) noted that "It is a peculiarity of the starling kind that they fly in flocks and wheel round in a sort of circular ball, all making towards the center of the flock." Selous (1931) organized many years of anecdotal observations of cluster flocks and framed the basic question, "There does not appear to be an identifiable leader in such groups, so how do these birds coordinate their movements?" Selous's speculative hypothesis was "thought-transference," and he viewed a coordinated flock as a kind of group mind. Selous was handicapped by lack of a conceptual model that would permit the formation of testable hypotheses and an almost total lack of quantitative information. On the other hand, Heppner and Haffner (1974) presumed that there *had* to be a leader in such flocks, and then proceeded to demonstrate the formidable obstacles to visual or acoustic communication between such a putative leader and its followers.

Synchrony, or apparent synchrony, in the turning movements of cluster flocks has drawn much attention. Observers describe a "flash" that passes, wave fashion, through the flock, and conclude from this that the turn is initiated in one part of the flock and then spreads. Gerard (1943) observed that birds that were pacing his car at 35 mph turned within 5 msec of each other. Unfortunately, like many early studies, the details were vague; we do not know what kind of birds were involved, nor how the determination was made. Potts (1984), Davis (1980), and Heppner and Haffner (1974) describe waves of turning in European Starlings, suggesting the existence of some originating point for the turn, or a possible follow-the-leader model. Heppner and Haffner (1974) expressed the time lag between the initiation of a turn by a leader on one side of a spherical flock, and a subsequent turn by a follower taking his cue to turn by the sight of the leader turning, as a function of the reaction time of individual birds, and the diameter and density of the flock. Potts (1984) suggested a "chorus-line hypothesis" to explain a rapid wave of turning in cluster flocks. In this hypothesis, turning birds respond not to turning neighbors, but to more distant birds. In other words, they anticipate the approaching wave of motion.

However, there is a possibility that observers who have seen a wave of turning may, in fact, have seen instead an artifact of the way that a stationary observer perceives the turn. Birds, like fish, do not reflect light uniformly over their bodies. Starlings have semireflective feathers, and the shorebirds reported in other

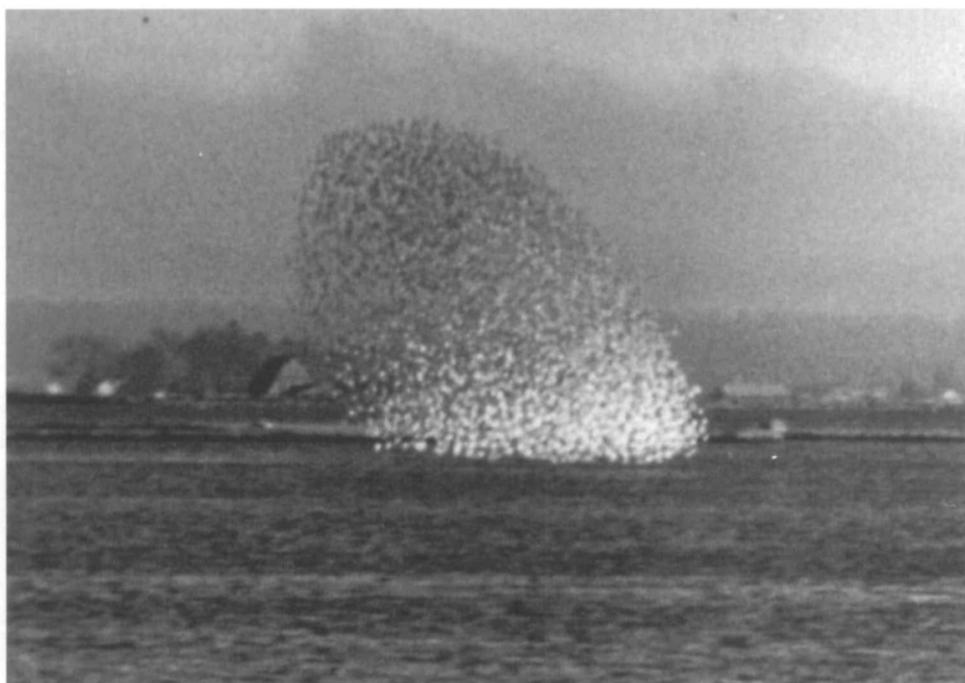


Figure 5.5. How simultaneous turns might give the impression of a “flash,” or wave of turning. In a dense flock of Dunlin, birds turning catch the light off their bodies, creating a wave of white that passes through the flock. (Photograph by Betty Orians.)

studies are also differentially colored. If a ground observer was watching a group of birds that were turning simultaneously, the “flash” might appear first in one portion of the flock, then give the impression of moving through the flock as the flock’s position in three-dimensional space changed relative to the observer and light source (Fig. 5.5).

Davis (1975) investigated another apparent simultaneity in take-off of a flock of pigeons. Using “actor” and “observer” pairs, the “actor” was induced to take off with a mild shock. Observers departed within .5 msec, unless the “actor” displayed some preflight intention movements before the shock, in which case its flight tended to be ignored.

5.3.2 Analysis

Major and Dill (1977) provided the first determination of the three-dimensional structure of freely flying bird flocks: European Starlings and sandpiper-like Dunlin, *Calidris alpina*. In this and a later paper (Major & Dill 1978), they used a

stereoscopic technique that employed two synchronized still cameras mounted on a rigid, 5 m bar. Although they were able to determine interbird distances, there was not enough information to determine flight paths of individual birds. Major and Dill concluded that the internal organization of the cluster flocks they studied strongly resembled that of minnow schools (Pitcher 1973); that is, nearest neighbors tended to be behind and perhaps below a reference fish. Dunlin had a tighter, more compact flock structure than Starlings, somewhat surprising because the Dunlin had flight speeds approximately two to three times faster than the Starlings. One might rather expect that at higher flight speeds, more distance between birds would be desirable for collision avoidance.

Pomeroy (1983) and Pomeroy and Heppner (1992) described a technique for plotting the three-dimensional locations and flight paths of individual pigeons in flocks of twelve to twenty birds using two orthogonally placed synchronized 35-mm still cameras focused on a common point (Fig. 5.6. See Appendix for a description of their method). Although their method of data reduction involved making photographic prints and measuring locations with calipers, the basic technique could be easily modified to use video and a digitizer or video framegrabber.

Being able to plot flight paths over time allowed a more detailed examination of the dynamic structure of cluster flocks. Pomeroy and Heppner (1992) found that birds regularly shifted position within the flock (Fig. 5.7). Birds in front ended up toward the back, and birds on the left ended up on the right at the completion of a turn. This rotation of position was a consequence of the birds flying in similar-radius paths, rather than parallel paths during the turn, suggesting that no individual bird was the "leader." The possibility still exists that there might be a kind of rotating positional leadership although there is no evidence for such a mechanism at this time.

Pomeroy (1983) suggested that flocking birds are more easily able to transit through the interstices between neighbors than fish can move between individuals in a school. In most of Pomeroy's trial flocks, nearest neighbor distances decreased during a turn.

Progress in the analysis of cluster flocks was slow, not so much for a lack of analytical tools, but (until recently) the lack of a conceptual alternate to a leadership model to produce coordinated movements. Presman (1970) was committed to a leader model, but refined Selous's (1931) "thought transference" model to a more sophisticated model in which electromagnetic fields produced by either the brain or neuromuscular system of the leader would be instantaneously transmitted to other members of the flock, there to act either on the follower's brain or directly on the follower's neuromuscular system. The flock would then become a kind of "superindividual." Neither of these hypotheses had any experimental

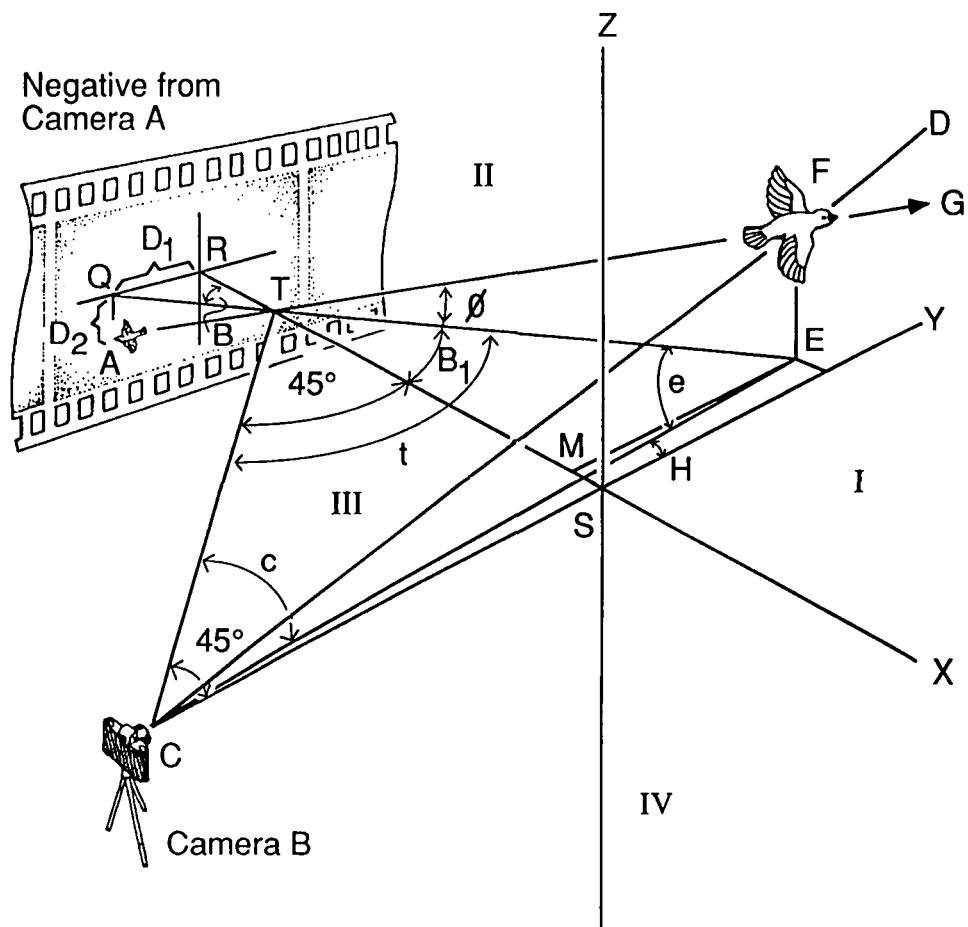
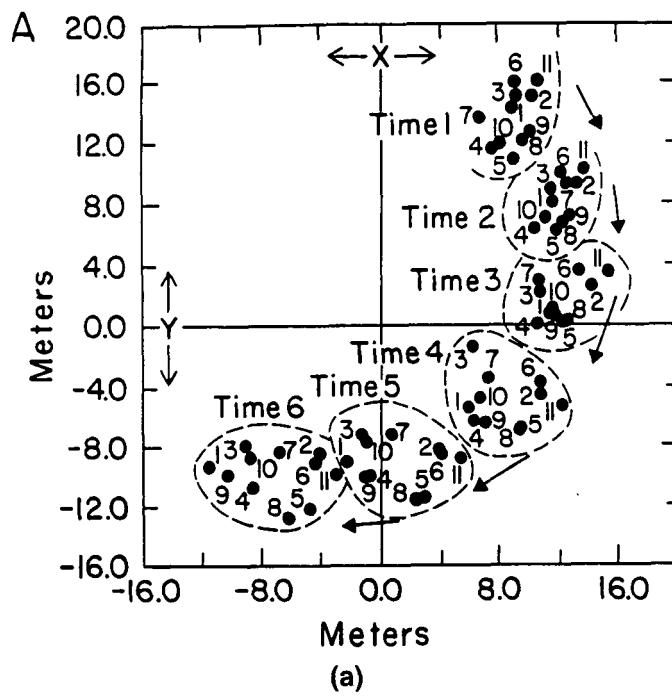


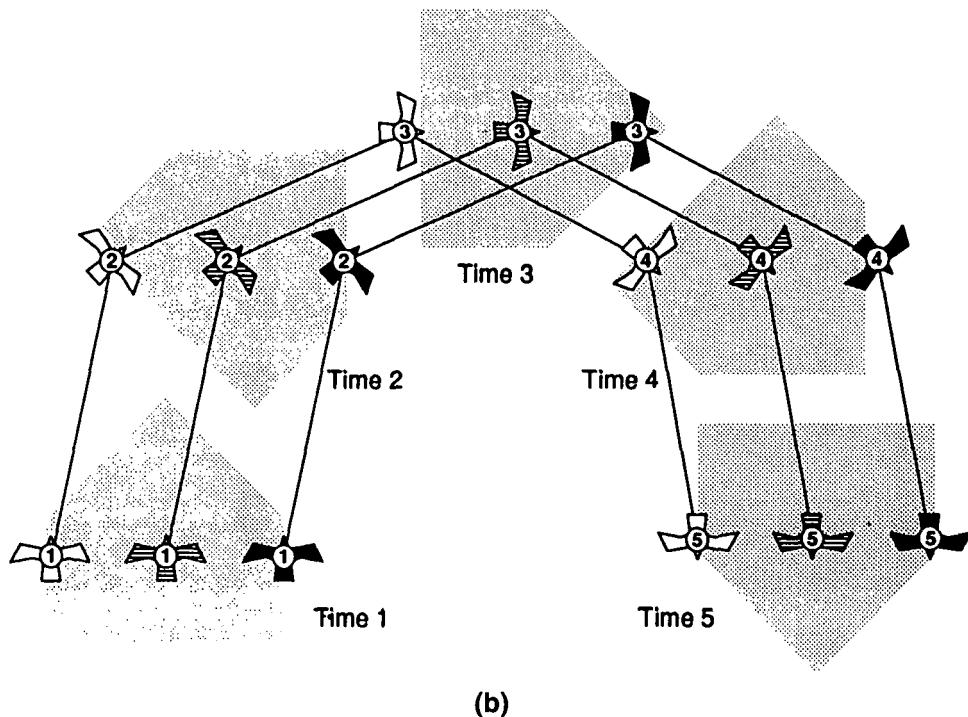
Figure 5.6. Nonstereo determination of three-dimensional location of individual birds. Two cameras, A and B, are aimed at, and equidistant from a common point, S, that represents the center of a sphere of radius, CS, that represents the maximum volume in which a bird's location may be determined. Point T is the projection of the bird's position in three-dimensional space (from Pomeroy & Heppner 1992).

support and stretched biological communication to or perhaps beyond the limit, but there was then no biologically plausible nonleader model available either.

Although it is traditional to think of the internal architecture of cluster flocks in terms of potential adaptive significance, there are difficulties presented by some generally accepted suggestions for the adaptive advantage of tight, highly coordinated, and polarized flocks. For example, if coordinated flocking is of advantage against predation by hawks (Tinbergen 1951), why then do European Starlings turn and wheel in highly coordinated fashion for a half-hour to forty-five minutes above a roost before retiring for the night, exposing themselves to what would appear to be an unnecessary risk of predation? Wynne-Edwards



(a)



(b)

Figure 5.7. (A) Two-dimensional projections of each individual numbered pigeon in a flock at 650 msec intervals. Birds rotate their positions in the flock during the turn. (B) Demonstration of how flight on paths of equal arc will result in position shift within the flock (from Pomeroy & Heppner 1992).

(1962) suggested that these movements served to inform individuals how big their population size had grown, but it is hard to see why it would take almost an hour of flight a day to serve this purpose.

Because of these problems, by the early 1980s, publication about cluster flocks had almost dried up, with the exception of Davis's (1980) and Potts's (1984) descriptive accounts of turning. As more has been learned about the behavior of complex dynamic systems, however the possibility arises that behaviors that are enigmatic in adaptive terms may in fact be interpreted as emergent properties that are the outcome of more fundamental physical or mathematical properties of the system itself. By the mid-1980s, it appears that a *zeitgeist* was at large, because working independently, and approaching the subject from very different disciplines, three investigators raised the possibility of a nonleader, nonadaptive (at least directly) model that could account for the coordinated movements of flocks. Okubo (1986) published a theoretical paper suggesting that coordination in flocks might be achieved by the application of the mathematics of nonlinear dynamics. Heppner (1987) suggested that flocking might be an emergent property arising out of simple rules of movement followed by individuals in the flock. Reynolds (1987) and Heppner and Grenander (1990), working independently, developed computer flock simulations in which the flock was a self-organized structure. Both models used the basic principles of attraction and repulsion to direct the movements of individuals.

Heppner and Grenander's (1990) simulation was based on a stochastic differential driven by a Poisson process with associated random variables equations.

$$dv_i(t) = (F_{\text{home}} + F_{\text{vel}} + F_{\text{interact}})dt + dP(t) \quad (5.1)$$

$$v_i(t) = du_i(t), \quad i = 1, 2, \dots, n$$

where $u_i(t) = (x_i(t), y_i(t))$ is the location of bird number i at time t .

The equation incorporated the following assumptions and variables:

A. Attraction toward a central place.

The model was based on the behavior of starlings, whose most highly coordinated flocks appear near an attraction such as a roost, or feeding area. Therefore F_{home} expresses a tendency toward an attraction. As a bird draws closer to the perimeter of the attraction, it is more strongly attracted until it crosses the perimeter, at which time the influence of the attraction drops to zero. This relationship was expressed for the i th component.

$$F_{\text{home}}^{(i)} = -u_i(t)f_{\text{home}}(u_i(t)); \quad i = 1, 2, \dots, n \quad (5.2)$$

where u_i is the vector from the homing zone to bird i , f_{home} is a scalar valued function, and t_0 is the minimum radius of a circular attraction area.

B. Velocity regulation.

If individual birds in a flock tend to have the same velocity, the chance of overrunning, or being overrun, is minimized. However, an individual bird might depart from the mean velocity of its neighbors to avoid collision with a neighbor intersecting its flight path, or its velocity might be affected by physical factors such as gusts of wind. After such perturbations, it was assumed that individuals would return to a “preferred” velocity. In nature this would be determined by the collective behavior of the flock, but in the model it could be varied by the experimenter. The velocity control term was expressed as

$$F_{\text{vel}}^{(i)} = -v_0(t)f_{\text{vel}}(v_i(t)), \quad (5.3)$$

where v_0 is the preferred velocity.

C. Interaction between birds.

The spacing that individuals might choose to maintain between themselves and neighbors might be influenced by collision-avoidance requirements, communication, aerodynamic considerations, and predator avoidance to name a few. The model assumed that individuals would integrate the spatial requirements of these factors and arrive at a preferred distance to neighbors. Birds closer than the preferred distance would be repelled in proportion to their proximity to neighbors. Birds above, but close to, the preferred distance would be strongly attracted to a neighbor. However, this attraction would decrease with increasing distance, eventually dropping to zero. The later provision allows the flock to split into two or more subflocks – a phenomenon often seen in nature.

If $d_{ij}(t)$ means the vector difference from individual i to j , $d_{ij}(t) = u_j(t) - u_i(t)$ the i th component will be:

$$F_{\text{interact}}^{(i)}(t) = \sum_{j=1}^n f_{\text{interact}}(d_{ij}(t))d_{ij}(t) \quad (5.4)$$

The interaction dies out if the interindividual distance $d_{ij} > d_r$

D. Random impact.

The fourth term $dP(t)$ was originally included with the idea of more closely simulating a natural environment in which wind gusts, distractions from moving objects on the ground, and predators might randomly perturb the flight paths of in-

dividuals. In practice, without the inclusion of this term, it was not possible to produce a coordinated, polarized simulated flock, an interesting observation in terms of both the dynamics of the model system and the transitions between coordinated and uncoordinated flocks in nature.

The random impact term was modeled by an n -dimensional, time-homogeneous Poisson process with stochastically independent components. The i th component of $dP(t)$ was zero unless t happened to be an event of the i th component of the Poisson process. In the latter case, $dP(t)$ equals a random three-vector with uniformly distributed components, with a scalar parameter controlling the magnitude of the random vector.

Heppner and Grenander's (1990) model produced polarized flocks that would either orbit an external attraction and demonstrate the rotation of individual position seen in Pomeroy and Heppner's (1992) natural pigeon flocks, or escape the influence of the attraction and fly a straight flight path indefinitely, depending on the values attached to the variables in the model, such as preferred spacing. The model would not, however, produce the spontaneous coordinated turns seen in natural flocks.

Heppner and Pakula (unpublished) prepared a computer simulation of a type of natural flock behavior that resembles, in basic character, a simultaneous, or near-simultaneous, departure from a wire or field, and thus bears resemblance to a coordinated, or near-synchronous turn. In this behavior, flocks of blackbirds will descend to a field and forage. From time to time, individual birds will "pop up" spontaneously to a height of a few meters above the ground (Heppner & Haffner 1974). Occasionally, a bird will depart the area after "popping up," but more typically will settle back to the ground. From time to time, small groups will pop up and leave, but after a variable interval, the entire flock will appear to rise up simultaneously and move to a new foraging area.

In Heppner and Pakula's two-dimensional model, an individual bird is represented by a graphic "bird" that can move freely on a Y axis line above the X axis ground surface. At the beginning of the demonstration, birds are spaced equidistantly along the ground surface. Each bird is a member of a cohort of birds that are within a defined lateral distance from a bird in question. The cohorts overlap.

At the beginning of a run, individual birds pop up randomly in space and time. The mean interval between pop-ups can be varied by the experimenter. When a bird pops up, it rises to a height on the screen where it can "see" the other birds in its cohort. If no other birds in its cohort are in the air, or if the number of other birds in its cohort who have also spontaneously popped up and are airborne are below a preset threshold, the popped-up bird will slowly descend back to the ground. If, however, the threshold number is exceeded, the bird will depart the area by flying vertically off the screen.

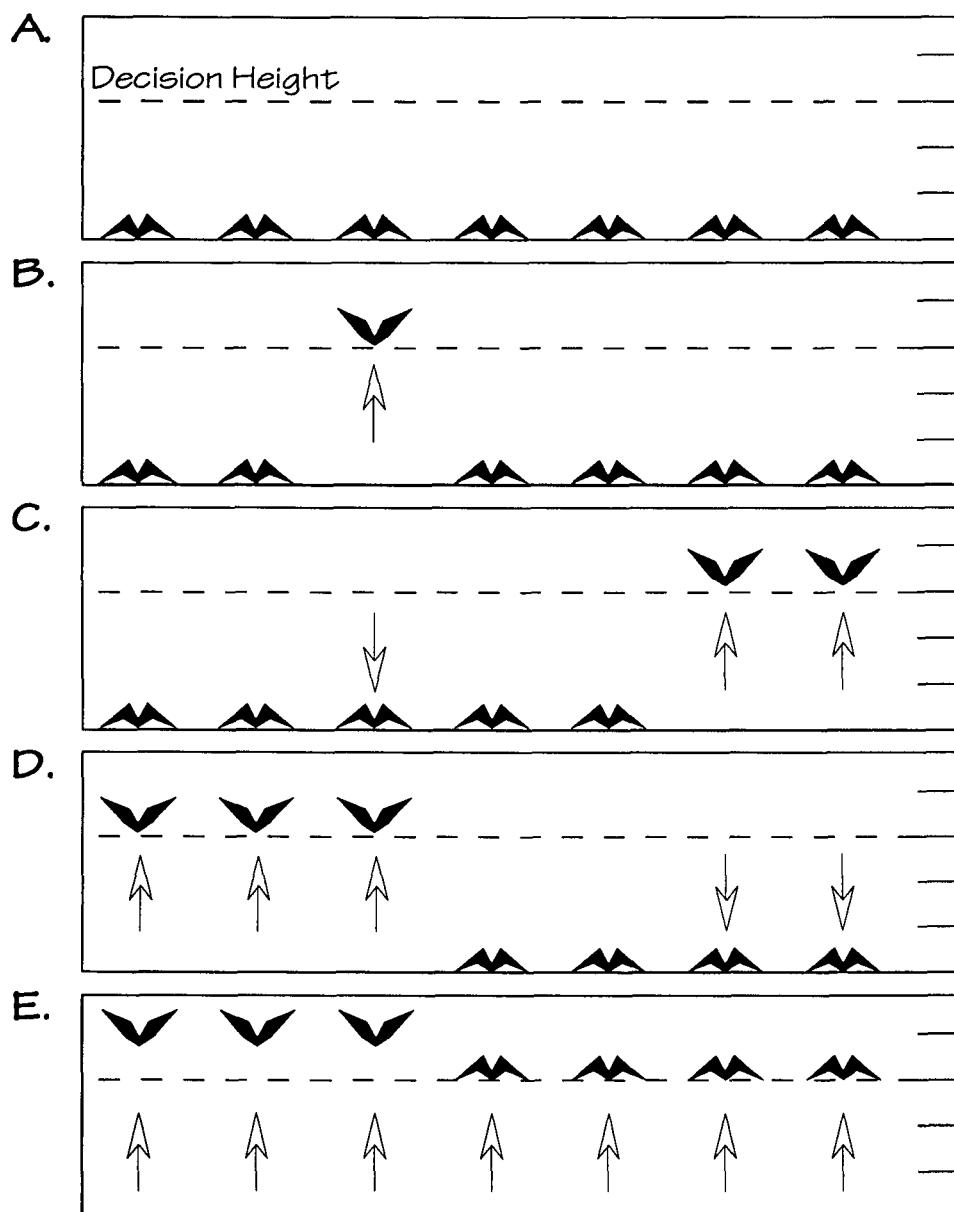


Figure 5.8. Demonstration of a “pop-up” model. (A) All birds are on the ground. (B) One bird randomly flies above the decision height, detects no other birds, and (C) returns to ground as two other birds which happen to be next to each other in the same cohort randomly “pop up” above the decision height, but seeing no other birds, (D) return to ground as three birds which happen to be in the same cohort randomly “pop up,” and seeing a threshold number of their cohort above the decision height, (E) fly away, as other birds on the ground see a cohort depart and depart themselves.

Birds on the ground will ignore popped-up birds in the cohort, unless the number of birds in the air exceeds a threshold, in which case all of the birds in the cohort will rise simultaneously and depart the area. Birds not in the cohort in question will ignore the behavior of birds in other cohorts, unless the number of cohorts in the air exceeds a preset threshold, in which case all birds in the flock rise up and depart the area (Fig. 5.8).

By manipulating the thresholds, it is possible to produce qualitatively a behavior that resembles natural flocks; individuals pop up at random, usually dropping back to the ground, small groups rise up and leave without affecting the flock as a whole, and after a period of time, the balance of the flock rises up almost simultaneously and departs.

A similar mechanism might be employed to produce coordinated turns in a flock. In natural flocks, individuals and small groups are constantly turning away from the flock as a whole. Sometimes they return, other times they do not. Individual birds might have a threshold for being influenced by neighboring turners; if only a few neighbors turn at random, they will be ignored, but if a greater-than-threshold number turns, the individual will follow the turners. In this case, coordinated turns, like the formation and cohesion of the flock itself, might be driven by a stochastic process.

5.4 Future directions and problems

Low-tech, inexpensive techniques now exist for determining the two- and three-dimensional structure of bird flocks, but they require so much time for manual data reduction that few people would now be willing to employ them. High-tech, expensive methods exist that would solve the data-reduction problem, possibly even permitting real-time three-dimensional analysis, but there remains the problem that essentially killed wide use of radar ornithology – cost and availability. The perfect three-dimensional analysis technique does not currently exist for bird flocks, but if it did, it would have the following properties:

1. Portability. Whether using stereo (e.g. Major & Dill 1977), or orthogonal (e.g. Pomeroy 1983) techniques, present optical methods require a relatively fixed volume of space within which the birds can fly. This greatly reduces the usefulness for the analysis of wild flocks. Ideally, one should be able to set up and take down a recording device in ten minutes or so, to take advantage of blackbird or shorebird flocks whose appearance is unpredictable.
2. Auto-correspondence. To date, three-dimensional analysis methods require images from at least two matching viewpoints. A technique that would permit

rapid, automatic, and accurate correspondence of the images would be very valuable.

3. Low initial cost and data-acquisition cost. Most footage obtained of wild animals in the field is worthless for one reason or another, so many feet of film or tape must be exposed. Cine film is very expensive now, but offers excellent resolution, and true slow motion. Videotape is very cheap, but has only a fraction of the resolution of 16-mm film, and with consumer camcorders, does not permit true slow motion.

Perhaps more important than the development of a faster, cheaper, and better analytical technique is resolving the question of what to measure with this technique (see discussion by Dill et al. Ch. 14). What parameters should be measured to address questions of leadership, synchrony, internal structure, and driving mechanism? How do you define a “turn”? Is it when more than a certain fraction of the birds depart from the mean flight path of all birds by a given angular amount? Is the interval between turns significant in some way? To use an ornithological metaphor, there is a chicken-and-egg problem here. Without knowing what the technique has the capacity to measure, it is difficult to set the task for the technique, and without the technique, it is difficult to know what questions can be addressed with it.

Ultimately it will be desirable to “truth-test” the models and simulations that have been made. It is all well and good to prepare a stunning and realistic computer simulation of a flock, but how do you know real birds are using a similar algorithm? To test this, it will be necessary to measure parameters in both the simulation and the real flock, and with some appropriate statistical test, compare them. At this stage in the development of the field, it is not clear what the key parameters should be, so perhaps a shotgun approach might be in order, in which every parameter that *can* be measured by a technique (such as interbird distances) *is* measured in both simulations and flocks, to see which offer promise for identifying characteristic flock properties of particular bird species.

Model-makers still have much to learn from their models. Heppner and Grenander (1990) noted that the values of the parameters in their model that produced flocking behavior were arrived at serendipitously, and the choice of a Poisson-based force rather than a Gaussian one to drive the model was fortuitous rather than deliberate. In essence, the model worked, but it was not altogether clear why. Attraction–repulsion models (Warburton & Lazarus 1991) may be useful in investigating flock formation. Studying the properties of a flocking model at a screen may permit avian investigators to have the same facility in testing hypotheses as, for example, students of schooling have had in looking at fish in a tank.

In summary, the three major immediate tasks that must be addressed in the analysis of the structure and dynamics of bird flocks are (1) the development of an inexpensive, portable device for determining three-dimensional space positions of free-flying individuals over time, and whose data can be reduced directly by computer; (2) the determination of what parameters to measure in either a real flock or a model, or both, that will speak directly to questions of leadership, synchrony, initiation of turning and takeoff, internal structure, and coordinating mechanism; and (3) a complete and thorough analysis of the properties of existing simulations to determine what factors influence the formation and movements of simulated flocks.

Acknowledgments

I thank Susan Crider, who did most of the yeoman work in the library, and C. R. Shoop, J. G. T. Anderson, and W. L. Romey, who read early drafts of this manuscript and offered helpful suggestions. J. Parrish did a wonderful job of reducing the manuscript by 20% without causing either hurt or outrage.

Appendix *Absolute position.*

Information derived from the two photographic prints was first used to establish where in three-dimensional space each bird in the flock was located each time photographic samples were taken. A Cartesian-coordinate system was defined for this point-in-space analysis. The X- and Y-axes of the system were perpendicular and crossed at the point of intersection of the optical axes of the two 35-mm cameras. The XY-plane was parallel with the ground. The Z-axis, or vertical axis, of the system was defined as perpendicular to the XY-plane. The elevation (Z-axis) and the bird's displacement along the horizontal grid system (XY-plane) were the real-space coordinates of the bird. Real-space coordinates were calculated for each bird in the flock for every point in time at which the flock was photographed. For the computer program developed to determine the positions of a bird, the horizontal and vertical deviations of a bird's image from the center of a negative were used as the basis for all calculations (Fig. 5.6).

The position of a bird on a negative from camera A can be used to locate that bird along a line originating and extending from point *T* (the optical center of the lens) to point *G* at infinity. The bird could be anywhere along line *TG*. Line *TG* is

determined as follows: The horizontal displacement (distance D_1) of the image of the bird's head from the center of the negative is measured to yield the length of side QR in triangle QRT . Side RT of the triangle is the focal length of the camera lens when focused at infinity (58 mm). Angle B in right triangle QRT can be expressed as $\tan^{-1}(QR/RT)$. Triangles QRT and MET are corresponding right triangles, such that angle B_1 in triangle MET is equal to angle B in triangle QRT . Angle B_1 in triangle MET defines the horizontal displacement of line TG on the Y axis. With this information only, the bird could be in quadrant I or II.

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

In the example shown in Figure 5.6, the photograph from camera B shows that the bird is left of the center line (Z -axis). In the view taken from camera A, the bird is also left of the Z -axis, placing it in quadrant II of the XY plane. Lines FE (Z -coordinate), ME (Y -coordinate), and MS (X -coordinate) must now be determined.

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

$$TE = [(TC) \sin(\angle c)] / \sin(\angle e) \quad (5.5)$$

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

$$TM = (ME)[\tan(\angle B_1)] \quad (5.6)$$

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

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

$$D = [(X_R - X_N)^2 + (Y_R - Y_N)^2 + (Z_R - Z_N)^2]^{0.5} \quad (5.7)$$

Subscripts R and N in the formula refer to the reference (R) and neighbor (N) birds. Each bird in the flock was analyzed in turn as the reference bird for every time at which the flock was photographed. Distances between each reference bird and all other birds in the flock were calculated to yield a series of values for first-nearest neighbor, second-nearest neighbor, through N th-nearest neighbor. Data for each of the neighbor-distance categories, and the associated mean values, were plotted over time to represent graphically the structure of the flock (Pomeroy & Heppner 1992).