AVIAN FLIGHT FORMATIONS

By Frank H. Heppner

Flight formations of birds are among the most widely observed, yet least understood phenomena in avian biology. Two recent ornithology texts (Welty, 1962; Pettingill, 1970) collectively devoted less than a page and a half to discussion of the functions of flight formation and possible mechanisms of coordination, aerodynamics, and other related factors. Vine (1971), Beer (1958), and Werth (1960) speculated on the advantages of flocking as social behavior, but the functions of the various types of flight formations have not received much consideration. This paper presents a working classification of different types of avian flight formations, and offers some suggestions on possible biological advantages of each type.

DEFINITIONS

Beer (1958) defines a flock as "... two or more birds which associate with each other due to innate gregarious tendencies." Emlen's (1952) flock definition is "any aggregation of homogeneous individuals regardless of size or density." Emlen's definition presents difficulties for the analysis of flight formations. For example, the term "homogeneous individuals" excludes groups of mixed blackbirds, which are commonly referred to as flocks. I propose to divide Emlen's definition into two parts, and offer for consideration that:

A FLIGHT AGGREGATION is a group of flying birds, lacking coordination in turning, spacing, velocity, flight direction of individual birds and time of takeoff or landing, assembled in a given area. An example would be a group of terns feeding on a school of fish.

A FLIGHT FLOCK is a group of flying birds, coordinated in one or more of the following parameters of flight: turning, spacing, velocity, and flight direction of individual birds, and time of takeoff and landing. Flight flocks may differ in degree of organization, from the highly organized types seen in dowitchers and other shorebirds to loosely coordinated flocks of birds, such as American Robins. Coordination may at times be a result of extrinsic factors, for example a group of gulls flying into a prevailing wind.

These definitions of flock and aggregation agree with general usage definitions to be found in Webster's 2nd International Dictionary.

LINE FORMATIONS

Line formations are flight flocks characterized by one or more groups of birds flying in a line or queue. Seen in larger birds, such as waterfowl and pelicans, line formations typically show a rather high degree of regularity in spacing and alignment. The types of line formations are as follows:

COLUMN (Fig. 1A). In this formation birds fly in single file along the flight path, one behind the other. The column can be seen in Brown Pelicans following a shore line, although pelicans, like many

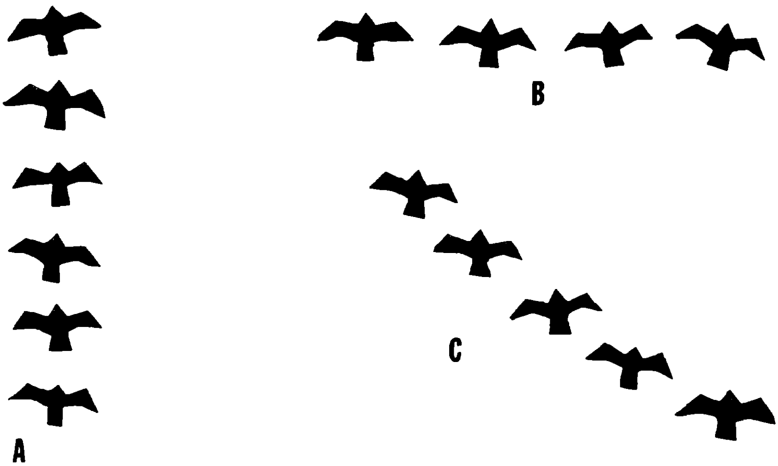

FIGURE 1. Line formations. A, column; B, front; C, echelon.

other birds, will shift from type to type of formation, depending on circumstances.

FRONT (Fig. 1B). In this formation, birds are aligned perpendicular to the direction of flight in a plane parallel to the earth's surface. I have seen this formation only as a momentary alignment in waterfowl as a transitional formation between other types.

ECHELONS (Fig. 1C). Birds in an echelon fly in single file, staggered stepwise from the bird in the lead position in the formation. Right and left echelons can be seen in waterfowl, the larger flocking waders, and pelicans, cormorants, and similar coastline-followers. Frequently a left echelon becomes a right echelon, and vice versa, by the expedient of a temporary breakup of the formation, rather than a swing from side to side.

J (Fig. 2A), and V (Fig. 2B). J and V formations are right and left echelons joined at the tip of the formation. V formations have approximately the same number of birds on each leg, whereas J formations are noticeably unbalanced. These formations are most commonly seen in waterfowl, although I have seen them in other large birds such as cormorants.

INVERTED J (Fig. 2C) and INVERTED V (Fig. 2D). The J and the V have a number of variations, usually seen less commonly then the primary types. In the inverted formations, the apex, or point of the formation is positioned at the rear. The inverted J and V occur sometimes in waterfowl, and usually represent a transition formation between one of the primary types. I have not seen this formation persist for long periods.

CLOSED LINE (Fig. 3A). In this formation, which is a special case of line formations, there is roughly a circular movement of birds following each other in line, differing from a simple aggregation in that a definite rotational tendency occurs. A closed line flock may rotate in either a clockwise or counterclockwise direction, and some-

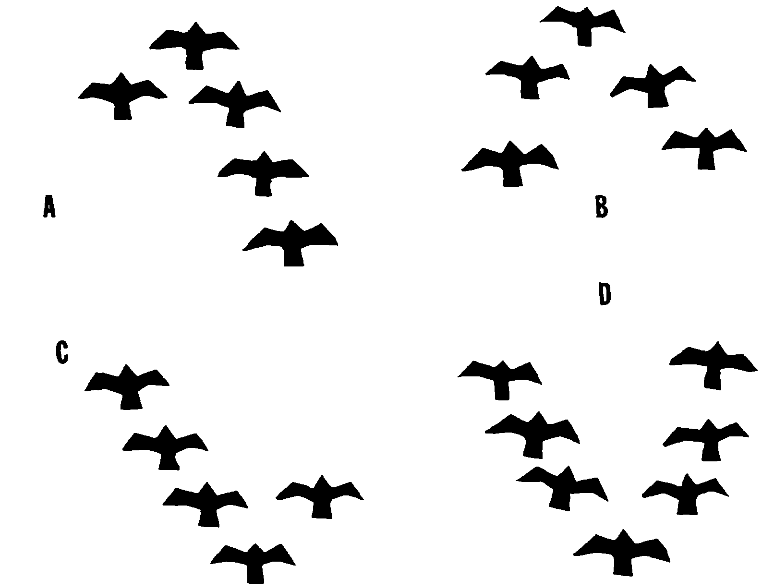

FIGURE 2. Line formations. A, J; B, V; C, inverted J; D, inverted V.

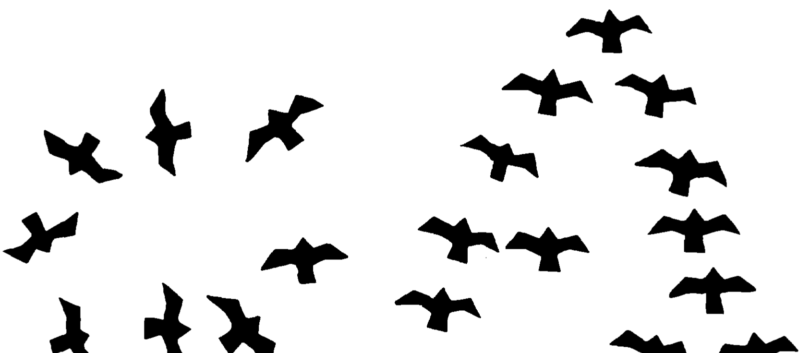

FIGURE 3. Line and compound formations. A, closed line; B, branched V.

times a second closed line formation occurs within the first, giving the visual effect of contra-rotating concentric circles. Closed line formations may be stacked above each other, and may be seen to best advantage in gulls circling over a dump or similar attraction.

COMPOUND LINE FORMATIONS

BRANCHED Vs AND Js (Fig. 3B). The Branched V is an example of a class of formations (V of Js, J of Vs, J of Js) in which there is a secondary branching from the main formation type.

VERTICAL ALIGNMENT

Line flocks may vary along the vertical axis. Birds at the head of the flock may be lower than, at the same level, or higher than birds toward the rear (Fig. 4A, 4B, 4C).

CLUSTER FORMATIONS

This class of formations presents a different aspect than the line or compound formations. In the former, one is impressed by the precision with which relatively small numbers of large birds maintain themselves in accurate spatial alignment and angular orientation with their neighbors, whereas in the cluster formations attention is drawn to the coordination that enables large numbers of small birds, flying in close order, to wheel and turn without suffering mid-air collisions. Cluster formations typically have a three dimensional structure. The functional significance of this class of formation may be quite different from that of either line or compound types.

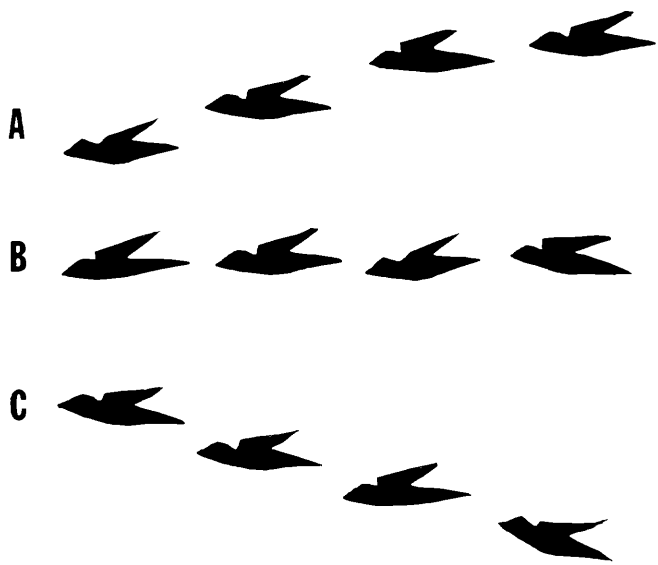

FIGURE 4. Vertical spacing in formations. A, ascending; B, level; C, descending.

GLOBULAR CLUSTER (Fig. 5A). I have borrowed a term from the astronomers to describe this formation, which is about as long as it is wide, and in three dimensional aspect, resembles an irregular spheroid. Birds that employ this formation will generally fly in apparent close order. It can most readily be seen in Starlings, blackbirds, sandpipers, and Brown-headed Cowbirds. When flying in this formation, birds can be seen making very rapid turns.

FRONT CLUSTER (Fig. 5B). This formation is broader than it is wide, with spacing and turning tending to be very precise. The front cluster is often seen in pigeons.

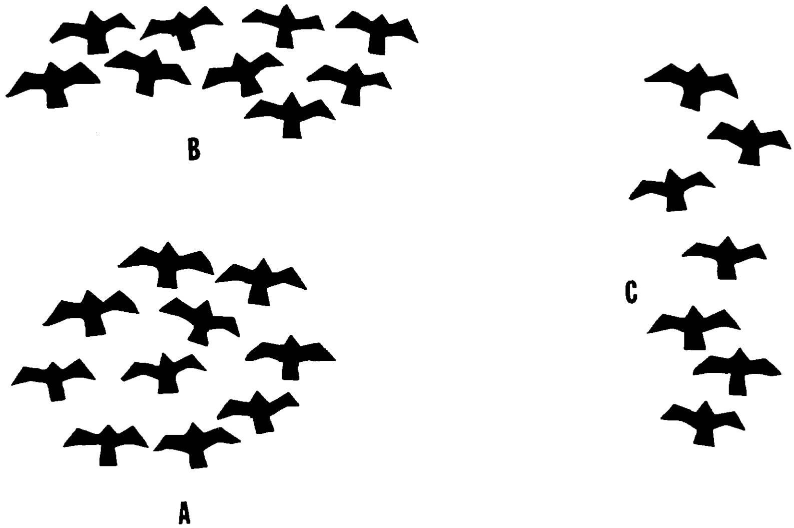

FIGURE 5. Cluster formations. A, globular; B, front; C, extended.

EXTENDED CLUSTER (Fig. 5C). An extended cluster is an oblate spheroidal formation, with the long axis parallel to the direction of flight. Extended clusters tend to be rather disorganized, with frequent breakoffs, and shifts of position. A typical example might be American Robins heading toward a nightly roost. This formation, in fact, may simply be a flight aggregation, birds flying independently toward a common destination.

These categories do not include all possible flight formations, as there are intergrades between most of the major types. Also, other formations, especially cluster types, defy simple description and do not have distinctive characteristics.

DISCUSSION

Although every ornithologist and bird observer has seen most, if not all, of the formation types described above at some time during his career, amazingly little is known about their functional significance, taxonomic distribution, ontogeny, or evolution. This void is due in part to the lack of technology needed to ask the important questions. The ornithologist until now could but helplessly shrug his shoulders when asked by the layman, "Why do geese fly in Vees?", or "Do blackbirds really all turn together, and if so, how do they all get the turning message at once?"

A few intriguing notes are found in the anecdotal literature. Gerard (1943) observed that unidentified birds in a flock which was pacing his car at 35 mph (56 kmph) apparently wheeled all at once, or at least within 5 msec of each other, although it is not clear how he made such a precise determination. Gerard did not observe any evident leadership in the flock. Nichols (1931) proposed that the bunching and wheeling of dowitcher and plover flocks served to hold the flock together until faster and slower individuals had adjusted speeds.

Most of the other available information pertinent to the question of flight formations deals not with flight formations per se, but with the adaptive significance of flocking in general. Vine (1971), for example, developed a model system for a group of terrestrial organisms pursued by a predator using visual detection methods, and proposed that in that situation, the most probable flock shape is a tight circle. Emlen (1952) discussed some of the social forces that draw birds together in flocks and regulate spacing between individual birds. Ainley (1972) described the flocking of Adelie Penguins (*Pygoscelus adeliae*) in terms of their spacing under various conditions. Ainley's work may be important in analyzing flight cluster formations, because coordination, spacing, and turning in penguins may not be related to aerodynamic factors.

An aerodynamic advantage resulting from formation flying has been discussed by several authors. Lissaman and Schollenberger (1970) proposed that in one type of line formation, the V, an aerodynamic advantage is gained by an individual bird by maintaining a particular wingtip-to-wingtip distance, and by angular positioning relative to other birds in the formation to capture tip vortex energy from the wings of neighboring birds. Cone (1968) argued, on grounds of aerodynamic theory, that the tip vortex arising from a flapping wing should not resemble that flowing from the fixed wing typical of aircraft. Gould (1972) reported that the mean distance between Canada Geese (*Branta canadensis*) flying in a Vee was 4.1 m (SD = 0.88) and suggested that measurements of the actual airflow conditions around a bird's wingtips will be needed to determine if the tip vortex travels in an appropriate direction and contains enough energy to make flying in V formation advantageous from the standpoint of capturing otherwise lost tip vortex energy. Tucker's (1968) techniques of flying birds in wind tunnels might well be adapted toward this end.

It is not necessary to propose that close formation flight might be aerodynamically advantageous only by virtue of ease in capturing tip vortex energy. Franzisket (1951) argued that tip vortex energy was not significant, and that close formation flying provided an area of turbulance-free air for flight, and close visual communication for flock members. Von Holst (1952) agreed with Franzisket and pointed out that (at that time) a phase relationship in wingbeats of birds flying in linear formations had not been demonstrated. A phase relationship in wingstrokes had been proposed by Geyr von Schweppenburg (1952) as being necessary for an hypothetical aerodynamic advantage. Nachtigall (1970) demonstrated a phase relationship between wingbeats of neighboring birds in flocks of geese, using cinema analysis techniques. Gould (1972), however, found no in-phase relationship in the wingbeats of Canada Geese flying in V formation, and suggested that each bird acted as an independent oscillator. Gould also found that the angle between the "legs" of the V ranged between 28° and 44°. These measurements should be valuable in resolving the question of an aerodynamic advantage to

V formation flight, once the characteristics of the airflow around the birds are known. Eichner (1954) compared the turning movements and formations of pigeons with similar alignments of war planes in combat formations.

Two major classes of questions are raised by formation flying. The first group of questions concerns the line formations, especially columns, echelons, and Vs. These formations are associated with large birds. We do not see sparrows or warblers flying in Vs, nor do we see blackbirds or other small birds that routinely travel in large groups flying in columns. If the advantage to be gained by flying in a line formation is aerodynamic, why is there not a strong correlation between flying in linear formation and necessity for energy economy on long flights? The small land birds flying long distances over water, apparently do not fly in linear formations, but cormorants do. If, as Lissaman and Schollenberger (1970) argue, substantial energetic advantages are gained by flying in precise, line formations, one would expect those flocking birds most severely pressed for energy to demonstrate a high degree of linear formation use. This does not seem to be the case. Clearly the question of the aerodynamics of formation flying cannot be resolved, in the face of conflicting or incomplete hypotheses, until data are obtained on the air flow conditions around birds flying in close formation.

Alternate hypotheses for explanation of characteristics of line formations are possible. Hamilton (1967) proposed that the V is advantageous for communication, in that the V allows a high degree of visual communication with neighboring birds, at the same time leaving a clear field of view to the front. In addition, Hamilton proposed that flying in a flock assisted navigation by averaging the direction preferences of individual birds, although Keeton's (1970) experiments on orientation and homing in single pigeons and small flocks do not support this view. Another possibility is based on the fact that the eyes of many birds that employ line flocks (and other birds, as well) are relatively immobile and are positioned laterally on the head. In order for an image to fall on the fovea of the eye, if the bill of a flying bird were pointed in the direction of flight, an object would have to be ahead of, and to the left or right of the bird in question. The V or echelon might then simply be the line configuration that allows each bird in the formation (with the exception of the leader) the opportunity to keep the image of its neighbor in maximum resolution, while at the same time permitting the head to be pointed forward. The V or echelon would then be a response to the necessity for maintaining a high resolution visual image of neighboring birds.

J. P. Hailman (pers. comm.) has suggested that aerodynamic factors related to the size of the organism may have a bearing on the apparent correlation between large bird size and flight in line formation. Differences in flight speed have significant effects in low speed aerodynamics due to differences in Reynolds' number, and it may be that the speed of the birds flying in line formation is the factor which has been significant in the evolution of this formation type.

A frequent observation in goose flocks is that the leading bird will occasionally, give up its position to another bird. The untested hypothesis offered by hunters, and others, is that the lead bird is cleaving a path through the air, the action presumably tiring, and must exchange this arduous task with another bird in the formation. Again, an alternate hypothesis is possible. The lead bird in a Vee or echelon has less opportunity to assess the state of the formation than any other bird, because all other birds are behind it. With forward directed eyes, the lead bird would have to turn its head to determine visually if the rest of the formation was still there. Assuming that it is desirable to insure that the flock stays together, the act of turning the head repeatedly at an angle to a 40-50 knot relative wind might well be tiring and call for relief. Conversely, the stimulus fatigue involved in looking for some time at the same neighbor in the formation might impel a bird back in the formation to change positions, or even assume the lead. Stimulus fatigue is certainly not unknown in animals, both at a simple neuronal level and at the more complex levels, such as sexual behavior (Beamer et al., 1969), and might well be a consideration here.

Cluster formations present a different set of problems. The most spectacular aspect of these formations also presents the most perplexing question. Do the birds actually turn at the same time when they wheel, and if so, how is the turning message transmitted simultaneously to all birds? A corollary question concerns the initiation of a turn. Individuals and small groups are constantly breaking off from the main formation, effectively eliminating the possibility that the turn is initiated by the first bird to change direction randomly. The stimulus for the initiation of a turn might be a sound signal given by an individual leader; this seems unlikely, given the din of massed blackbird and Starling flocks. A "follow-the-leader" principle might be used, the entire flock visually mimicing the movements of a leader, but this would present problems in flocks of tens of thousands or more. Finally, other means of communication hitherto undiscovered, perhaps involving electromagnetic fields, might be employed (much as ultrasonic communication in bats and marine mammals was unknown only a generation ago).

It may be significant that the greater the density of the flock, the greater is the apparent precision of turning and movements Heppner, pers. obs.). If the birds are flying loosely together, as in extended or front clusters, there is little danger of collision, and a follow-the-leader type of directional guidance would be sufficient to explain the movements of the formation. As the formation becomes tighter, the danger of collision increases, and coordination of movement becomes more important. Coordination would be important in tight formations not only in turning and wheeling, but also in wing flapping. It would be interesting to test the reaction times of birds that display a high degree of coordination in formation, such as plovers and sandpipers, versus birds such as warblers, which are rarely, if ever highly coordinated in formation.

Study of flight formations in birds reveals many unanswered questions that might be addressed with the methods of modern technology, such as telemetry and radar. There is an additional bonus in that the flight formations of birds are among the most aesthetically pleasing aspects of avian life.

SUMMARY

Flight formations of birds are classified as flight aggregations, line flocks, compound flocks, and cluster flocks. These major categories are then subdivided and described. Possible functional advantages for each major formation type are discussed. Alternate hypotheses of aerodynamic advantage or facilitation of visual communication are examined for line formations represented by the V formation of waterfowl. Problems of coordination in cluster flocks are discussed.

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LITERATURE CITED

Ainley, D. G. 1972. Flocking in Adelie Penguins. *Ibis*, **114:** 388-390.

Beer, J. R. 1958. The composition of bird flocks. *Flicker*, **30:** 78-83.

Beamer, W., Bermant, G., and M. T. Clegg. 1969. Copulatory behavior of the ram, *Ovis aries*. II: factors affecting copulatory satiation. *Anim. Behav.*, **17:** 706-711.

Cone, C. C. 1968. The aerodynamics of flapping birdflight. Special Scientific Report No. 52. Virginia Inst. Marine Sci.

Eichner, D. 1954. Formationsflugregeln auch beim Flug der Haustabe. *Vogelwarte*, **17:** 15-18.

Emlen, J. T., Jr. 1952. Flocking behavior in birds. *Auk.*, **69:** 160-170.

Franzisket, L. 1951. Über die Ursachen des Formationsfluges. *Vogelwarte*, **16:** 48-55.

Gerard, G. W. 1943. Synchrony in flock wheeling. *Science*, **97:** 160-161.

Geyr v. Schweppenburg, H. 1952. Vorteile der Zuggeselligkeit. *Vogelwarte*, **16:** 116-119.

Gould, L. L. 1972. Formation flight in the Canada Goose, (*Branta c. canadensis*). M.S. Thesis, Univ. Rhode Island.

Hamilton, W. J., III. 1967. Social aspects of bird orientation mechanisms. *In* Animal orientation and navigation, (R. M. Storm, ed.) Oregon State University Press, Corvallis.

Holst, E. v. 1952. Diskussionsbemerkung. *J. Ornithol.*, **93:** 191.

Keeton, W. T. 1970. Comparative orientational and homing performance of single pigeons and small flocks. *Auk*, **87:** 797-799.

Lissaman, P. B. S., and C. A. Schollenberger. 1970. Formation flight of birds. *Science*, **168:** 1003-1005.

Nachtigall, W. 1970. Phasenbeziehungen der Flügelschläge von Gansen während des Verbandflugs in Keilformation. *Z. vergl. Physiologie*, **67:** 414-422.

Nichols, J. J. 1931. Notes on the flocking of shore birds. *Auk*, **48:** 181-185.

Pettingill, O. S., Jr. 1970. Ornithology in laboratory and field. Minneapolis, Burgess Publishing Co.

TUCKER, V. A. 1968. Respiratory exchange and evaporative water loss in the flying Budgerigar. *J. Exp. Biol.*, **48**: 67-87.

VINE, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behavior. *J. Theor. Biol.*, **30**: 405-422.

WELTY, J. C. 1962. The life of birds. Philadelphia, Saunders.

WERTH, I. 1960. The problem of flocking in birds. *Proc. XII Intern. Ornithol. Congr.*, **6**: 744-748.

Department of Zoology, University of Rhode Island, Kingston, R. I. 02881.

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