AN ANALYSIS OF FUNCTION IN THE FORMATION
FLIGHT OF CANADA GEESE

JOHN P. BADGEROW[1]

Department of Biology, Syracuse University, Syracuse, New York 13244 USA

ABSTRACT.—I analyzed formations of Canada Geese (*Branta canadensis*) with a single, direct method of testing predictions from multiple hypotheses. The results support both energetic (aerodynamic) advantage and orientation communication through visual contact as functions of this complex behavior. Comparison of observed positioning patterns with criteria for optimal function suggests priority may be given to the maximization of energy savings within limits imposed by environmental and other constraints. *Received 14 November 1986, accepted 10 July 1988.*

FORMATION flight is widely observed yet poorly understood. The planar, diagonal line formations of Canada Geese and Snow Geese (*Chen caerulescens*) can be observed across the continent, especially during their migratory seasons. Two major functions have been proposed for this distinctive flight pattern. The *energetic advantage* hypothesis states that formation flight reduces energy costs relative to solo flight. It is based on the application of aerodynamic formation flight theory to avian formations (Lissaman and Shollenberger 1970). The *orientation communication* hypothesis holds that a formation permits the most advantageous use of the combined orientation experience of the flock by facilitating visual communication among members (Hamilton 1967, Heppner 1974).

Gould and Heppner (1974) pioneered the use of projective geometry in a test of these functional hypotheses. They measured the actual distances between neighboring birds in formation lines or legs. Their analysis of Canada Goose formations suggested that distances were too great for a nontrivial energetic advantage and supported the orientation communication hypothesis by default. Unfortunately, the distances reported were not appropriate for evaluation of energy savings. A reanalysis of their results indicated that formation members realized up to 51% in energy savings over solo flight (Badgerow and Hainsworth 1981). O'Malley and Evans (1982) analyzed formation flight functions in American White Pelicans (*Pelecanus erythrorhynchos*), and found support for both

hypotheses. They applied a variety of approaches to the interpretation of function, some of which yielded ambiguous results. For example, wingbeat frequency was used as a simple indicator of relative energy savings although aerodynamic power is a complex function of wingbeat frequency, wingbeat kinematics, and flight velocity (Rayner 1981). A lower frequency does not necessarily translate into less work.

My goal was to evaluate how extensively Canada Geese maximize the proposed advantages of formation use. I developed a uniform method of testing multiple predictions within a common analytic framework. Distinctive predictions of flight behavior were derived directly from each functional hypothesis, a nonfunctional hypothesis for formation geometry, and a null hypothesis. The geometry of positioning within diagonal line formations (including vees, jays, echelons, and others; Heppner 1974) can be described by a right triangle with acute angles at adjacent birds in a diagonal line (Fig. 1). The proposed advantages can be maximized by optimization of different elements of this basic triangle. Positioning was defined with respect to the bird ahead and can vary by movement in only 3 ways: along the flight path (depth), normal to the flight path (wing-tip spacing), or both. Each hypothesis predicts a characteristic flight behavior pattern in the form of a depth vs. wing-tip spacing relationship. Comparison of observed with predicted relationships provides immediate, primary evidence relevant to all hypotheses simultaneously.

METHODS

I examined the relationship between depth and wing-tip spacing (WTS) at a single instant for geese in each of 50 formations. Birds were filmed with a
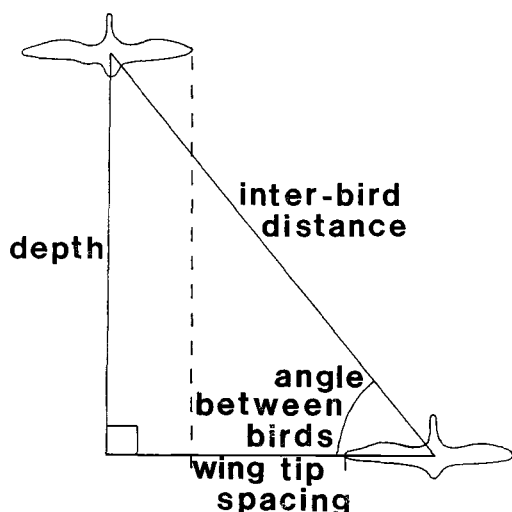

Fig. 1.   A right triangle geometry of formations.

Bolex 16 mm cine camera during morning flights at
Montezuma National Wildlife Refuge, Seneca Falls,
New York, in the spring (March–May) and fall (Oc-
tober and November) migratory periods of 1979. True
formation angles (angle between diagonal lines or
legs) and relative inter-bird distances (separation of
neighbors along legs) were obtained from films by
projective geometry (described in Gould and Heppner
1974, after Slaby 1966). An important exception was
in the method for establishing positions along a leg.
Bird centers lying near but not directly on a regres-
sion line (representing a leg) must be transferred to
the line to determine inter-bird distances accurately.
Gould and Heppner made this transfer parallel to the
y-axis. I transferred centers perpendicular to the bi-
sect of the formation angle (also parallel to the y-axis)
to obtain inter-bird distance for depth, but parallel
to the bisect to obtain inter-bird distance for WTS
(Fig. 2). This modification improved the accuracy of
positioning measurements for WTS and allowed the
independent measurement of depth and WTS. Inter-
bird distances were calculated to the nearest 0.1 m
using body length for scale. The right triangle be-
tween each pair of adjacent birds (see Fig. 1) was
solved from inter-bird distance and the angle at the
bird ahead (one-half the formation angle). This yield-
ed actual depth and WTS measurements.

PREDICTIONS

Energetic advantage.—The energetic advantage hy-
pothesis implies optimization of the base of the tri-
angle. The length of the base is determined by WTS,
the measure of position within the field of upwash
generated by the outboard wing of the bird ahead
(Lissaman and Shollenberger 1970, Badgerow and
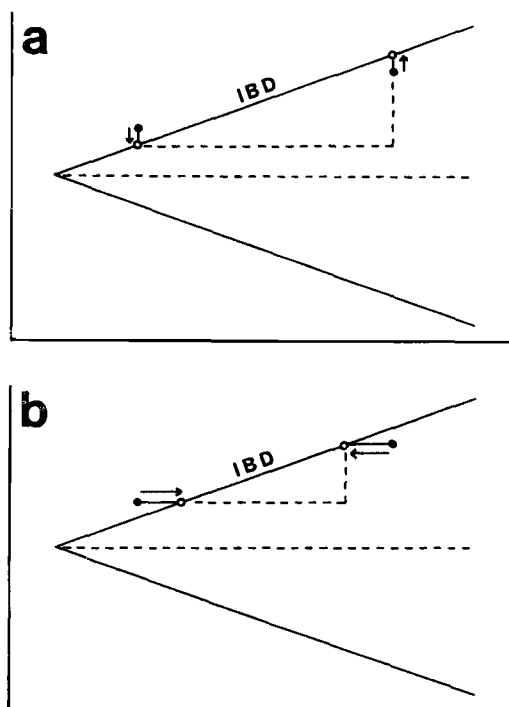Hainsworth 1981). Optimizing WTS can maximize the

Fig. 2.   Method of transfer of bird center points to
regression lines. (a) Transfer perpendicular to the bi-
sect yields inter-bird distance (IBD) for determination
of depth or displacement along the flight path. This
is similar to Gould and Heppner's (1974) method of
transfer parallel to the y-axis. (b) Transfer parallel to
the bisect yields inter-bird distance for determination
of WTS or lateral displacement. Solid circles are the
bird center points and are in the same positions in
(a) and (b). Open circles are transferred points.

augmentation of lift (or reduction of drag) relative to
solo flight and reduce energy cost. Ideally, WTS should
remain constant at the optimal position with variation
in depth (Fig. 3a). Realistically, the prediction is no
relation between depth and WTS with WTS less vari-
able than depth.

Maximum savings of about 50% over solo flight are
available at a WTS of −0.16 m (i.e. an overlap of wing
tips of 0.16 m; Badgerow and Hainsworth 1981). The
prediction remains the same regardless of the precise
location of the optimal WTS position. The near-max-
imum range is narrow and savings decline asym-
metrically as a negative power function of distance
in either direction from the optimal position. Savings
also decline with increasing depth but this effect is
trivial over the range of depths observed.

This hypothesis is based on a fixed-wing analog for
avian formation flight (Lissaman and Shollenberger
1970). Fixed-wing and flapping-wing wakes are never
identical but they can be considered functionally

equivalent for species with large wing spans, shallow wingbeats, and a slow wingbeat rate relative to flight speed, when cruising in a level, steady flight mode (Higdon and Corrsin 1978, Alexander 1982). These requirements are clearly met by the Canada Goose (Cone 1968, Van Wormer 1968, pers. obs.). Rayner's (1979, 1980) analysis of the vortex wake of birds further confirms the validity of the fixed-wing analog for species, such as the Canada Goose, that generate lift on the upstroke as well as downstroke of the wingbeat cycle.

Orientation communication through visual contact.—Visual communication of orientation experience may be best at a specific angle between birds (see Fig. 1). The angle is determined by the arrangement of certain retinal features (*area centralis* and fovea) and by the angle between the visual axes (straight lines passing from the fovea through the center of the lens of each eye). Adjusting the angle between birds could cause the image of the bird ahead to fall within the *area centralis* and directly on the fovea, which are retinal regions of maximum optical resolution (Pumphrey 1961, Sillman 1973). This positioning would provide the most efficient communication of change in flight path and velocity. Molodovsky (1979) found a pattern of general agreement between flock structure and visual anatomy among 48 avian species. To maintain an optimal angle between birds, variation in depth and WTS must be in the same direction (both increasing or both decreasing, Fig. 3b). The prediction is a direct relation between depth and WTS.

Unfortunately, there is no detailed description of retinal features in the Canada Goose. Heppner et al. (1985) stated that the retina "appeared to be afoveate" but did not mention the *area centralis* and did not describe the retina in detail. They may not have fixed the retina quickly enough to prevent its typically rapid necrosis upon death. All others of the Anatidae examined have features congruent with this hypothesis (Pearson 1972). The evidence seems insufficient to accept *Branta canadensis* as anomalous. Further, even if there is no single foveal pit, there could be a broader optimum that would still influence formation geometry as predicted.

The functional hypotheses are not mutually exclusive, although they are mutually restrictive in their demands on positioning. A formation showing a direct relation between depth and WTS, with WTS less variable than depth, would indicate simultaneous support for both hypotheses (Fig. 3c). Formations may fail to indicate support for either functional hypothesis. A null hypothesis predicts no relation between depth and WTS with WTS more variable than depth. A horizontal line would be the extreme case (Fig. 3d). Formations supporting this null hypothesis are referred to as indeterminate.

Maneuverability and visual range.—An additional hypothesis is based partly on the observation (Poncy 1941) that, among species in diagonal-line formations,
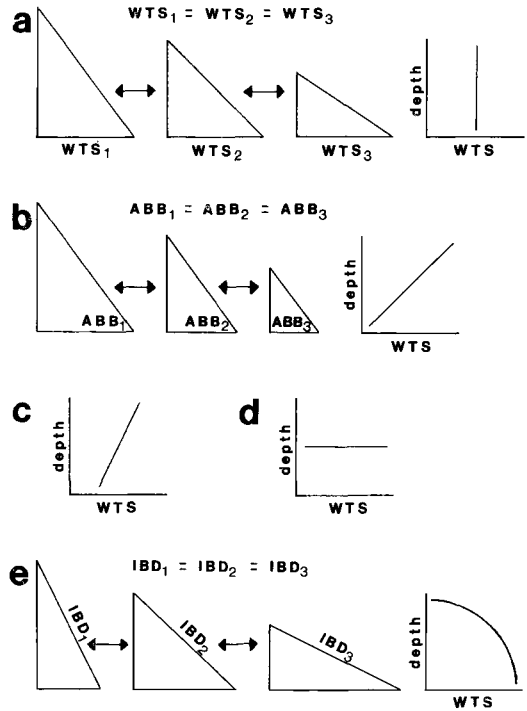

Fig. 3. Predicted relationships between depth and WTS for optimization of: (a) WTS, (b) angle between birds (ABB), (c) both simultaneously, (d) neither, (e) inter-bird distance (IBD).

the distance between individuals along a line (inter-bird distance, Fig. 1) tended to increase with length and wing span. There may be an optimal inter-bird distance to allow for variation in position while maintaining a coherent formation. The hypothesis implies further that the formation permits members simultaneously to see each other, straight ahead, and outboard of the flock. This is not a functional hypothesis. It can explain aspects of formation geometry but not why birds should fly in groups rather than solo. Optimization of inter-bird distance requires that depth and WTS vary in opposite directions. The prediction is an inverse relation; specifically, an arc (Fig. 3e).

RESULTS

A test of the 5 predictions required a measure of association between depth and WTS and a measure of their relative variability. Because most formations included 12 or fewer birds and skewness in WTS values was too prevalent to be ignored, the assumption of bivariate normal distributions required for the Pearson product-moment correlation coefficient could not be made (Sokal and Rohlf 1969, Daniel 1978). I
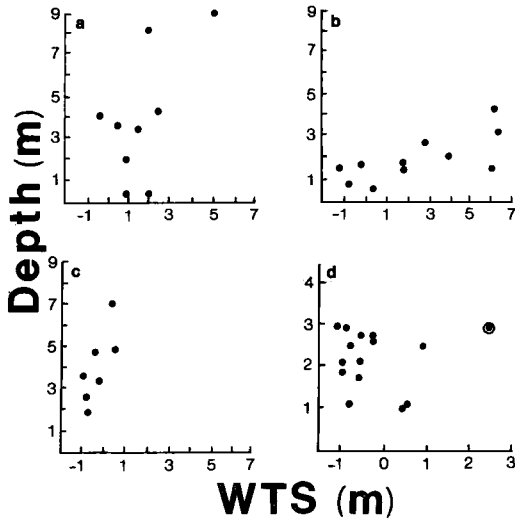
Fig. 4. Observed relationships between depth and WTS in formations that indicate optimization of: (a) WTS, (b) angle between birds, (c) both simultaneously, (d) WTS after deletion of the circled outlier.
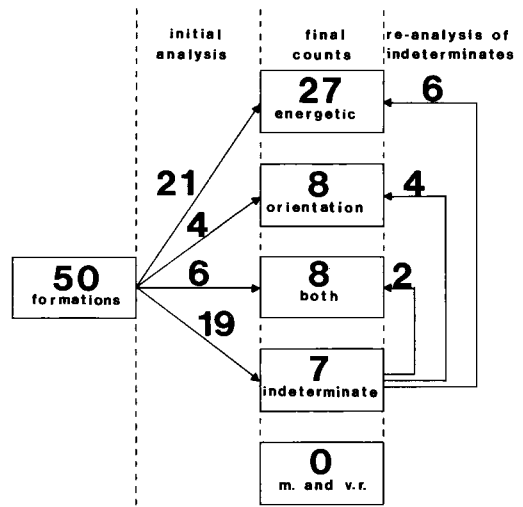

Fig. 5. Resolution of 50 formations into those that support the energetic advantage hypothesis, the orientation communication through visual contact hypothesis, both simultaneously, and neither (indeterminate). No formations supported the maneuverability and visual range (m. and v. r.) hypothesis.

used the nonparametric Spearman rank correlation coefficient (0.05 level of significance) as a measure of association. Relative variability was determined by comparison of quartile deviations, due to skewness and for consistency with the nonparametric statistics.

I analyzed 50 formations. The null hypothesis of independence could not be rejected in 40. WTS was less variable than depth in 21 of the 40, in support of the energetic advantage hypothesis (Fig. 4a). The remaining 19 were indeterminate. The orientation communication hypothesis was supported by a significant direct relation between depth and WTS in 10 formations. WTS was more variable than depth in 4 of these 10, which supported the orientation communication hypothesis alone (Fig. 4b). WTS was less variable than depth in the remaining 6, which showed simultaneous support for the energetic advantage hypothesis (Fig. 4c). None of the 50 formations showed the significant inverse relation required for support of the maneuverability and visual range hypothesis.

Decisions relied on small-sample statistics. Many of the decisions to classify formations as indeterminate were biased by as few as 1 or 2 members in positions distinctly anomalous with the formation pattern. Outlying observations may obscure an attempt to represent the population and conservative deletion is justified

(Barnett and Lewis 1978). Deletion of outliers can increase information yield. An outlier was defined as a bird in an extreme position in either WTS or angle between birds. No more than 20% of the birds in a formation were deleted. This level was chosen arbitrarily because it limited deletions to no more than 2 or 3 in most formations yet allowed at least 1 in smaller formations.

In each of the 19 indeterminate formations, an outlier was deleted and the formation reanalyzed. I repeated the process until the formation was no longer indeterminate or the limit for deletions was reached. Seven formations remained indeterminate. Of the other 12, 6 supported the energetic hypothesis (e.g. Fig. 4d), 4 supported orientation communication, and 2 supported both. The average fraction of members deleted in the 12 formations was 12.3%. The initial statistical analysis and reanalysis of the indeterminate formations gave final counts of formations for each hypothesis as summarized in Fig. 5.

DISCUSSION

Each formation member must track the movements of its predecessor to maintain optimal

position. Tracking may be accomplished by change in flight power requirement with variation in WTS (Lissaman and Shollenberger 1970) and visually. The inherent difficulty of flight coordination is compounded by the effects of turbulence and unpredictable change in wind direction and velocity. In view of these constraints, the observed level of variation in positioning was surprisingly small and implies a strong effort to maximize the advantages of formation flight. I suggest that both advantages are obtained but priority is given to energy savings.

The geese realized an average savings of about 10% over solo flight (determined from Badgerow and Hainsworth 1981, based on Lissaman and Shollenberger 1970). The advantage could translate as greater flight range, greater reserves at the end of a flight, or any other of the potential benefits of energy conservation. The only apparent associated cost is the requirement of cooperative behavior. Because animals operate on finite energy budgets, and energy can at times be critical to reproduction or survival, we might expect the use of energy-saving mechanisms which are sufficiently unconstrained. The energetic advantage of formation flight is valuable and may be especially important during migration.

There are compelling biomechanical reasons for the energetic advantage to be of particular significance for Canada Geese. The larger subspecies are among the heaviest of all flying birds. The power required per unit mass of flight muscle increases with body mass (Pennycuick 1972). Wingloading (mass/unit area of lifting surface) reflects the aerodynamic work required in flight. Canada Geese have a wingloading greater than that of the heavier Mute Swan (*Cygnus olor*) and 142 other species listed by Poole (1938). Energy-saving flight mechanisms other than formation use may be unavailable to Canada Geese. Most other migratory species with similar wingspans but reduced wingloadings will soar and glide (Pennycuick 1969). Cranes (Alerstam 1981) and pelicans (O'Malley and Evans 1982) soar in thermals, glide, and use formations on migratory and local flights. Canada Geese glide only when landing and apparently never soar, presumably due to high wingloading.

Sharing migration experience among formation members may also contribute to energy conservation. In spite of seasonal variations, Canada Geese migratory flights consistently follow the most direct path among stopover sites that meet requirements for food and open water (Wege and Raveling 1983). A less direct route would increase flight time and energy cost. Formations I studied were on local flights. Seven of the eight formations that supported the orientation communication hypothesis alone occurred in the fall. These flocks probably included young on their first migration. The presence of inexperienced geese in a formation could place a premium on orientation communication, even on local flights.

Evidence for orientation communication as a function of group movement can be found in a variety of species. Sand fiddler crabs (*Uca* spp.) appear to orient themselves according to their neighbors while moving (Herrnkind 1972). Orientation communication contributes to foraging efficiency in schooling fish (Pitcher et al. 1982) and bird flocks on the ground (e.g. Krebs et al. 1972). Homing Pigeons (*Columba livia*) may improve directional accuracy over solo flight by flying with others toward the same destination (Tamm 1980). Thick-billed Murre (*Uria lomvia*) leave a colony in diagonal line formations. The formation leader appears to monitor the heading of returning flocks and change course accordingly. Formation members follow the leader (Gaston 1987).

Environmental conditions constrain optimal positioning. Constraints were such that no effort to maximize an advantage was discernible in the 7 indeterminate formations. Multiple functions may often constrain one another. The functional hypotheses are not mutually exclusive. Consequently, most formations might show simultaneous support for both. The low incidence (16%) of support for both confirms the intensity of their mutually restrictive demands on positioning.

I found no effect of inter-bird distance among the formations studied. Spatial requirements for maneuverability and visual range in Canada Geese appear entirely compatible with optimal positioning for orientation communication or energetic advantage. In this respect, formation flight presents an informative contrast with fish schooling. Schools offer large energy savings with appropriate positioning (Weihs 1973). However, optimal positioning for hydromechanical advantage may be overriden by conflicting requirements for maneuverability and visual range (Partridge and Pitcher 1980, Partridge 1982). Certain prey species modified their

school from a pattern that favored energetic advantage to one that favored visual range when predators were introduced (Abrahams and Colgan 1985). Birds probably do not save energy through use of three-dimensional (nonplanar or cluster) flocks (Higdon and Corrsin 1978) but small species are vulnerable to airborne predation and modify their flock structure near a predator (Tinbergen 1951). Three-dimensional flocks resemble fish schools in structure and behavior (Major and Dill 1978).

LITERATURE CITED

ABRAHAMS, M. V., & P. W. COLGAN. 1985. Risk of predation, hydrodynamic efficiency and their influence on school structure. Env. Biol. Fish. 13: 195-202.

ALERSTAM, T. 1981. The course and timing of bird migration. Pp. 9-54 in Animal migration (D. J. Aidley, Ed.). Cambridge, Cambridge University Press.

ALEXANDER, R. M. 1982. Locomotion of animals. Glasgow, Blackie.

BADGEROW, J. P., & F. R. HAINSWORTH. 1981. Energy savings through formation flight? A re-examination of the vee formation. J. Theoret. Biol. 93: 41-52.

BARNETT, V., & T. LEWIS. 1978. Outliers in statistical data. Chichester, Wiley.

CONE, C. D., JR. 1968. The aerodynamics of flapping bird flight. Virginia Inst. Marine Sci., Spec. Sci. Rep. 52.

DANIEL, W. W. 1978. Applied nonparametric statistics. Boston, Houghton Mifflin.

GASTON, T. 1987. Seabird citadels of the Arctic. Nat. Hist. 96: 54-58.

GOULD, L. L., & F. HEPPNER. 1974. The vee formation of Canada Geese. Auk 91: 494-506.

HAMILTON, W. J., III. 1967. Social aspects of bird orientation mechanisms. Pp. 57-70 in Animal orientation and navigation (R. M. Storm, Ed.). Corvallis, Oregon State Univ. Press.

HEPPNER, F. H. 1974. Avian flight formations. Bird-banding 45: 160-169.

———, J. L. CONVISSAR, D. E. MOONAN JR., & J. G. T. ANDERSON. 1985. Visual angle and formation flight in Canada Geese. Auk 102: 195-198.

HERRNKIND, W. F. 1972. Orientation in shore-living arthropods, especially the sand fiddler crab. Pp. 1-59 in Behavior of marine animals, vol. 1 (H. E. Winn and B. L. Olla, Eds.). New York, Plenum.

HIGDON, J. J. L., & S. CORRSIN. 1978. Induced drag of a bird flock. Am. Nat. 112: 727-744.

KREBS, J. R., M. H. MACROBERTS, & J. M. CULLEN. 1972. Flocking and feeding in the Great Tit, Parus major: an experimental study. Ibis 114: 507-530.

LISSAMAN, P. B. L., & C. A. SHOLLENBERGER. 1970. Formation flight of birds. Science 168: 1003-1005.

MAJOR, P. F., & L. M. DILL. 1978. The three-dimensional structure of airborne bird flocks. Behav. Ecol. Sociobiol. 4: 111-122.

MOLODOVSKY, A. V. 1979. [Some peculiarities of vision in birds and their flock behaviour.] Zool. Zh. 58: 685-692.

O'MALLEY, J. B. E., & R. M. EVANS. 1982. Structure and behavior of White Pelican formation flocks. Can. J. Zool. 60: 1388-1396.

PARTRIDGE, B. L. 1982. The structure and function of fish schools. Sci. Am. 246: 114-123.

———, & T. J. PITCHER. 1980. The sensory basis of fish schools: relative roles of lateral line and vision. J. Comp. Physiol. 135: 315-325.

PEARSON, R. 1972. The avian brain. New York, Academic Press.

PENNYCUICK, C. J. 1969. The mechanics of bird migration. Ibis 111: 525-556.

———. 1972. Animal flight. London, Arnold.

PITCHER, T. J., A. E. MAGURRAN, & I. J. WINFIELD. 1982. Fish in larger shoals find food faster. Behav. Ecol. Sociobiol. 10: 149-151.

PONCY, R. 1941. Formations angulaires des vols de quelques espèces d'oiseaux migrateurs et les réactions observées (particulierement chez les canards). Ornithol. Beob. 1: 18-19.

POOLE, E. L. 1938. Weights and wing area of 143 species of North American birds. Auk 55: 511-517.

PUMPHREY, R. J. 1961. Sensory organs: vision. Pp. 55-68 in Biology and comparative physiology of birds, vol. 2 (A. J. Marshall, Ed.). New York, Academic Press.

RAYNER, J. M. V. 1979. A new approach to animal flight mechanics. J. Exp. Biol. 80: 17-54.

———. 1980. Vorticity and animal flight. Pp. 177-199 in Aspects of animal movement (H. Y. Elder and E. R. Trueman, Eds.). Cambridge, Cambridge University Press.

———. 1981. Flight adaptations in vertebrates. Symp. Zool. Soc. Lond. 48: 137-172.

SILLMAN, A. J. 1973. Avian vision. Pp. 349-387 in Avian biology, vol. 3 (D. S. Farner and J. A. King, Eds.). New York, Academic Press.

SLABY, S. M. 1966. Fundamentals of three-dimen-

sional descriptive geometry. New York, Harcourt, Brace, and World.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, Freeman.

TAMM, S. 1980. Bird orientation: single Homing Pigeons compared with small flocks. Behav. Ecol. Sociobiol. 7: 319–322.

TINBERGEN, N. 1951. The study of instinct. Oxford, Clarendon Press.

VAN WORMER, J. 1968. The world of the Canada Goose. New York, Lippincott.

WEGE, M. L., & D. G. RAVELING. 1983. Factors influencing the timing, distance, and path of migrations of Canada Geese. Wilson Bull. 95: 209–221.

WEIHS, D. 1973. Hydromechanics of fish schooling. Nature 241: 290–291.