

PRECISION AND DYNAMICS OF POSITIONING BY CANADA GEESE FLYING IN FORMATION

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SUMMARY

A method is described for reconstructing perspective-distorted film images of geese flying in V formations to allow measurements of wing tip spacing (WTS, the distance between wing tips of adjacent birds perpendicular to the flight path) and depth (the distance along the flight path between birds). Measurements for eight formations are used to test for savings in induced power from wing placement in a vortex field generated by other wings, using the model of Lissaman & Schollenberger (1970) to estimate savings. The median WTS for 55 geese corresponded to an induced power saving of 36%, about half the maximum possible. There was considerable variation in WTS between and within formations. Some birds maintained WTS close to an optimum for saving energy; others maintained WTS with excessive gap. Birds at the apex and those at large depths achieved low energy savings. Savings were enhanced by periodic changes in flight direction in response to variations in the position of the bird ahead. Individuals in some formations adjusted WTS more rapidly when they were displaced a greater distance from the optimum, and some position adjustments appeared to reflect the distribution of savings predicted from vortex theory.

INTRODUCTION

It has been suggested that the V formation flight of birds is an energy saving adaptation (Lissaman & Schollenberger, 1970; Hummel, 1978, 1983). Some aerodynamic models predict that birds may save up to 71% of induced power if they fly in an appropriate position in formation (Lissaman & Schollenberger, 1970), and preliminary analyses of the positions of Canada geese in formations indicate that the birds may achieve some benefits (Badgerow & Hainsworth, 1981; Badgerow, 1985).

The measurement used to test for energy savings is 'wing tip spacing' (WTS), the distance between wing tips of adjacent birds perpendicular to the flight path (measured as if the birds were line-abreast, see Fig. 1; Lissaman & Schollenberger, 1970; Hummel, 1978, 1983; Badgerow & Hainsworth, 1981; Badgerow, 1985). It measures the placement of wings within a vortex field generated by other wings. Energy savings depend on precision of wing placement in regions of the vortex field producing maximum lift. Savings also vary with the number of birds. For an 'infinite' number of birds, 71% saving in induced power has been predicted for

■ Key words: adaptation, energy savings, flight, geese, locomotion, vortices.

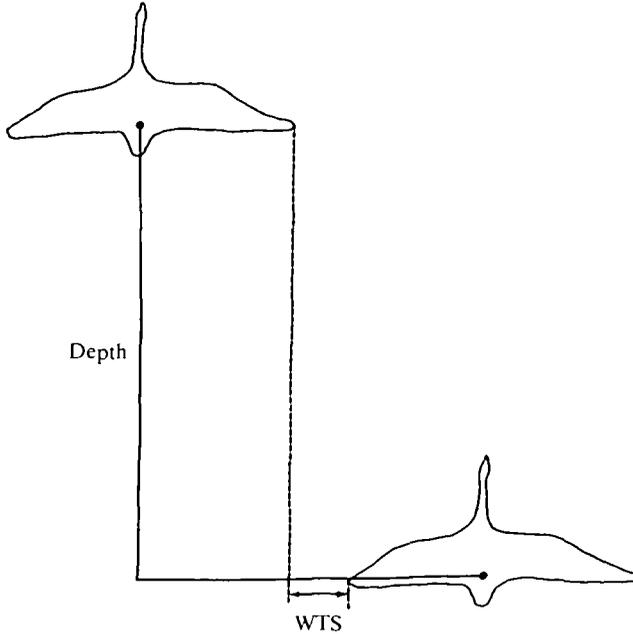


Fig. 1. Definition of wing tip spacing (WTS) and depth for adjacent birds in a V formation.

precise optimum positioning. A maximum of 51 % saving is predicted for a formation of nine birds (Lissaman & Schollenberger, 1970; Badgerow & Hainsworth, 1981).

Predicted savings depend on the model and assumptions used to estimate aerodynamic efficiency. Fig. 2 shows predicted savings for induced power for a formation of nine Canada geese based on a modification of the model of Lissaman & Schollenberger (1970) (Badgerow & Hainsworth, 1981). In the original model, only positive WTS values were considered, and savings were related to the wing tip spacing index:

$$R = b/b + s,$$

where b is wing span and s is wing tip spacing. To consider overlap of WTS, which is common in V formations, Badgerow & Hainsworth (1981) used the index:

$$R = b_{\text{EFF}}/b_{\text{ACT}} + s,$$

where b_{ACT} is the wing span of 1.5 m for a Canada goose, s is a positive or negative value for WTS, and b_{EFF} is an 'effective' wing span of $1.50 - 0.16 = 1.34$ m. With this index, savings are maximum at $s = -0.16$ m, the location of the centre of a vortex filament behind a steady wing of span 1.5 m.

The left side of Fig. 2 is not based on a calculation of available savings but is from the R index of Badgerow & Hainsworth (1981). However, under some conditions there would be a rapid decrease in savings with distance of overlap ($s < -16$ cm). If it is assumed that trailing vortices from both wing tips of the bird ahead are of equal strength, then the velocity field induced by the inboard wing ahead would produce an asymmetrical distribution of savings about $R = 1.0$. In this case, an overlap of 75 cm

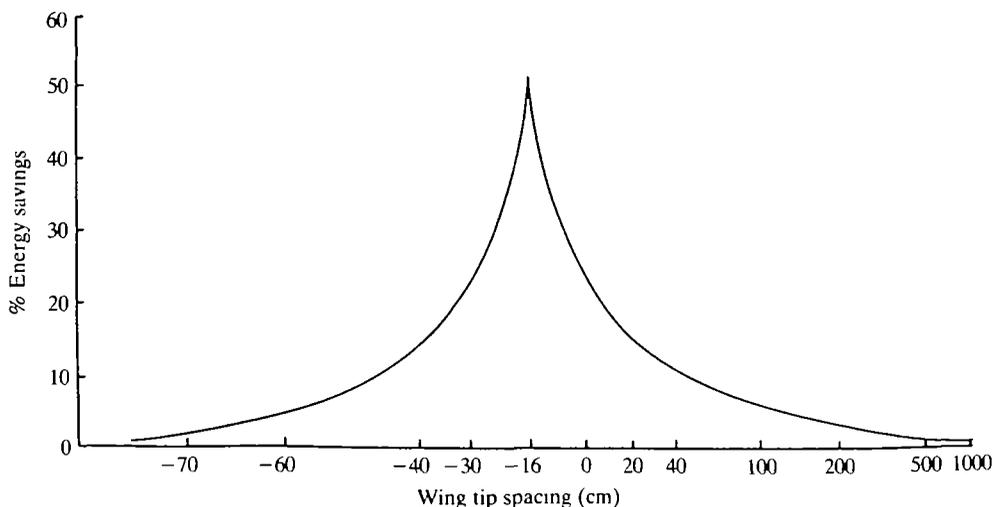


Fig. 2. Percentage positive savings in induced power at different wing tip spacings (WTS) for a formation of nine Canada geese (from Badgerow & Hainsworth, 1981). WTS less than -75 cm (half a span) would produce negative savings. See text for assumptions in estimating savings for WTS less than -16 cm.

or more by a trailing bird would place its inboard wing in a region of downwash from the trailing vortex of the inboard wing ahead. This should produce negative savings, and the highest induced drag would occur for birds flying directly behind others (Higdon & Corrsin, 1978). However, whether equal vorticity occurs for both wing tip vortices may depend on wing placement by the bird ahead. Ideally, precise positioning could result in no trailing vortex from the inboard wing ahead, since trailing vortices from opposite wings have opposite directions of circulation and could cancel each other out (Alexander, 1982). Less precise positioning could lead to trailing vortices of variable strength from inboard wings. A more refined analysis would be to calculate distributions of savings for overlap of WTS which depend on inboard trailing vortices of variable strength from variable precision of positioning of inboard wings. This has not been done.

The model is based on the additional assumptions that all birds fly in the same horizontal plane and wing movements are minor, so that steady wing conditions are sufficient to describe available savings. At slow flight speeds, vortices are shed periodically from the wings of birds (Rayner, 1979; Kokshaysky, 1979; Spedding, Rayner & Pennycuik, 1984). At high flight speeds, spanwise vorticity is continuous for kestrels (Rayner, 1985a) and bats (Rayner, Jones & Thomas, 1986), but there is vertical and horizontal variation from changes in wing positions during a beat cycle. This is likely to be the case for geese in formation flight, but I neglect this variation and assume a steady wing is sufficient, as a first approximation, to describe the position and strength of vortices. I thus estimate savings from predictions based on Lissaman & Schollenberger's theory. However, actual distributions of savings are likely to differ from those shown in Fig. 2, because of assumptions used to estimate

savings, variation in the position of vortices from wing movements, and/or variation in the vertical positions of individuals in formation.

For a Canada goose ($b = 1.5$ m) the predicted optimum WTS is to overlap the outboard wing ahead by 0.16 m (WTS = -16 cm). Note, however, that savings may drop dramatically near the optimum (Fig. 2). Slight variation in WTS in either direction could drastically lower benefits. This implies a high degree of precision flight to achieve maximum savings. I wished to determine if geese are capable of such high-performance flight. I present methods to measure WTS over time from analysis of the geometry of perspective distortion of film images. The results assess the extent to which geese performance matches optimal performance predicted by theory. I also try to identify features of flight which may contribute to and detract from the ability of individuals to realize the benefits of formation flight.

MATERIALS AND METHODS

Two methods have been used to reconstruct movements of flying animals with photography: (1) use of information on body dimensions to define geometry with single images, and (2) use of multiple images from non-coincident optical axes (see Rayner & Aldridge, 1985). The first was considered the only practical approach to filming Canada geese under natural conditions. Previous studies have used projective geometry to measure true positions (the view directly overhead) from a single film image taken when a formation was perpendicular to the camera (at camera maximum angle of inclination, Gould & Heppner, 1974; O'Malley & Evans, 1982; Badgerow, 1985). I extend these methods to analyse the film images taken on either side of the perpendicular to the camera.

A V is undistorted only when it is viewed directly overhead, so any image taken at other views must be corrected for distortion. This can be done in two stages: (1) by transforming the geometry along the flight path to the point where the V is perpendicular to the line of sight, and (2) by transforming geometry from this point to directly overhead. The two stages of this rectangular method are shown in Fig. 3 as transformation of a V from position A to B and then from position B to C .

Methods for the second stage have been described by Gould & Heppner (1974) and Badgerow (1985). The line of sight at position B (Fig. 3) is perpendicular to the base bisector and bisects the base bisector and both legs of an isosceles V . (The line of sight passes through the point on the interior of the triangle equidistant from the apex to the base and equidistant from both legs.) The base bisector appears smaller as distance increases, and the average length of a Canada goose (0.852 m, Gould & Heppner, 1974) can be used to correct its length. The V is transformed using the camera angle of inclination at the perpendicular to the flight path (Fig. 4). This widens the V angle and corrects the geometry to what would be seen directly overhead (Gould & Heppner, 1974).

The method for constructing isosceles V legs at the perpendicular is to assign x, y coordinates to the centre points of tracings of each magnified bird image and calculate a linear least-squares regression for each leg. V legs are made isosceles by

selecting a point behind the last bird in the longest leg and drawing a line to the other leg perpendicular to the angle bisector (which is coincident with the base bisector at the perpendicular). Points not on regression lines are translated there parallel to the

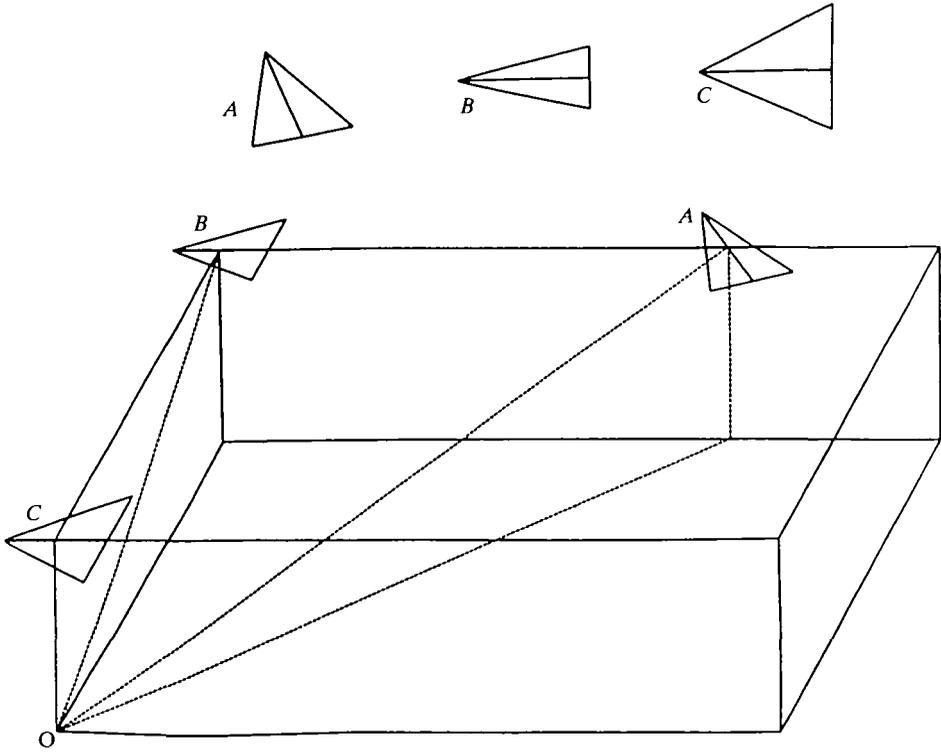


Fig. 3. Rectangular model for correcting perspective-distorted V images to the view directly overhead ($A \rightarrow B \rightarrow C$). The upper triangles represent plan views for an observer at O corresponding to the perspective views.

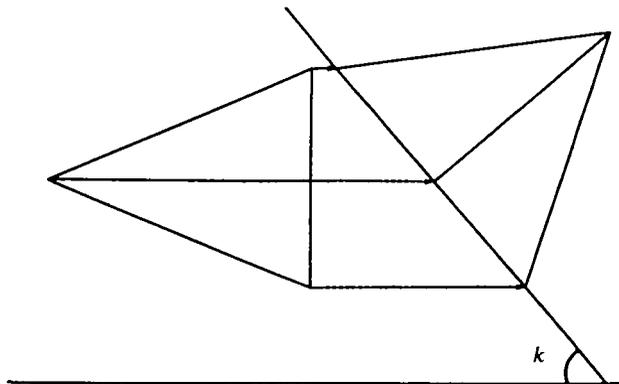


Fig. 4. Method for correcting V angle from the perpendicular to the view directly overhead. Angle k is the maximum angle of inclination (at the perpendicular to the flight path). The base bisector length is the same for each triangle (from Gould & Heppner, 1974).

base bisector to determine WTS (measured with respect to the bird ahead) and perpendicular to the base bisector to determine depth (the distance along the flight path between adjacent birds; Badgerow, 1985). This gives independent measurements for WTS and depth for each individual except the lead bird.

When a V is viewed away from the perpendicular, the image is rotated off the flight path (Fig. 3, A). The line of sight is to the centre of the base bisector and intersects the flight path at an acute angle. The line of sight intersects the image base bisector at a right angle since the eye or a camera is rotated to follow the V , but the orientation of the image base bisector is coincident with that of the true base bisector only at the perpendicular.

An isosceles V at the perpendicular is reconstructed using the geometry shown in Figs 5 and 6. Angle a is the angle of the line of sight to the flight path. Since the line of sight is perpendicular to the image base bisector, the latter is rotated through angle b ($b = 90^\circ - a$) from the flight path (Fig. 5). Rotating the V through angle b back to the flight path is equivalent to rotating the line of sight about the centre of the base bisector through angle b (Fig. 5). After rotation, the line of sight bisects both V legs and is parallel to the V base (as it is at the perpendicular where $a = 90^\circ$). Thus, the base bisector forms an acute angle a with the base (Fig. 5).

Fig. 6 shows a V rotated to the flight path where the base bisector is adjusted to be equal to its length at the perpendicular. Note that the leg which appears longer does so because the line of sight intersects it at a point greater than one-half the leg length at the perpendicular. It is distorted by doubling its length from the intersection without changing the angle between this leg and the base bisector. This is angle c (Figs 5, 6); it should not change as angle a varies. The V at the perpendicular will have an angle of $2c$.

Fig. 7 shows the orientation of bird lengths for a V away from the perpendicular. They parallel the V base bisector, so the base bisector is distorted by perspective and distance in the same way as bird lengths. Thus, the average length of bird images can be used to find the correct base bisector length.

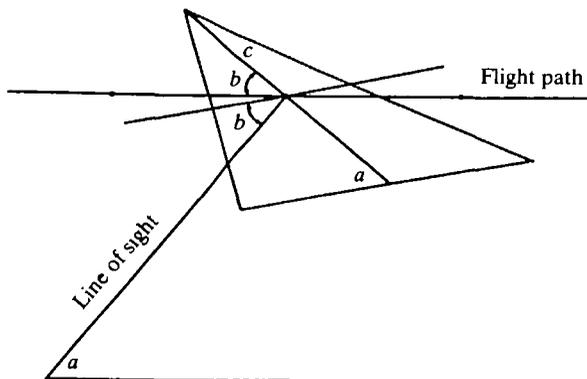


Fig. 5. Angles for a V for a plan view away from the perpendicular. See text for explanation.

Fig. 7 also shows the method for determining isosceles leg lengths distorted by perspective. A point is marked behind the last bird in the longest leg. The mid-point of this line is found and a line is constructed parallel to the other leg from the mid-point. This line will pass through the base at its mid-point. Construction of a base line from the end-point of the longest leg, with mid-point on the parallel line, and

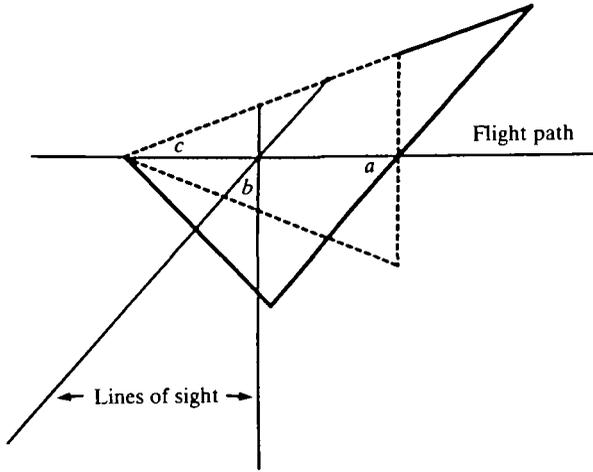


Fig. 6. Geometry for a plan view of a V at the perpendicular (dashed V) and away from the perpendicular adjusted to have the same base bisector length and orientation. Lines of sight are rotated through angle b and bisect the base bisector and both legs of the Vs for each view. Angle c remains constant and is used to reconstruct a V at the perpendicular.

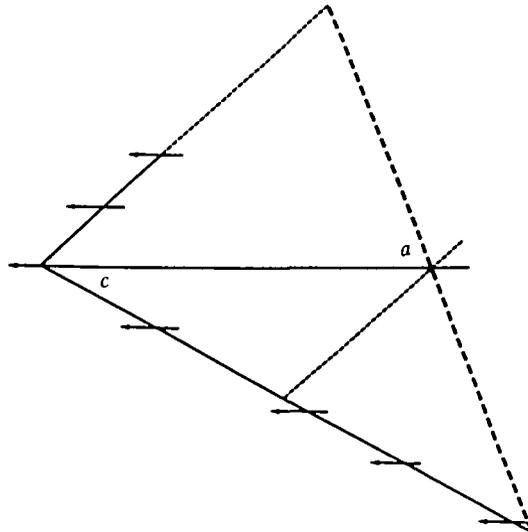


Fig. 7. Orientations of bird lengths (arrows) parallel the V base bisector. The intersection of the base and base bisector is positioned on the dashed line parallel to one V leg from the mid-point of the other. The base passes through the end point of the longest leg and forms angle a with the base bisector from the apex.

with angle a to the base bisector passing through the apex gives the isosceles V distorted by perspective. Each leg can then be reconstructed at the perpendicular by using the corrected base bisector length and angle c as components of a right-angled triangle. As with images taken at the perpendicular, V legs are constructed using linear least-squares regressions, and bird centre points not on regression lines are moved there parallel to the V base bisector to determine WTS and perpendicular to the V base bisector to determine depth (both measured with respect to the bird ahead).

For the rare case where a V passes directly overhead, angle a remains 90° and angle c varies with the inclination angle. The method for reconstructing the view directly overhead is simply to reverse the transformation shown in Fig. 4 (angle k becomes the camera angle of inclination).

I selected for analysis formations that appeared to follow a straight path, and I used the method shown in Fig. 8 to calculate angle a . I used two ciné cameras: a 16 mm camera with a 120 mm lens to film the formations, and an 8 mm camera with a macro lens to film an inclination scale attached to the tripod. The 8 mm camera was attached to an arm fixed to the top of the tripod. Both cameras were calibrated for filming speed ($12\text{--}18\text{ frames s}^{-1}$) by photographing a stopwatch. The cameras were activated synchronously so each V image frame had a measured inclination. The inclinometer was zeroed with a plumb line after the tripod had been levelled with a spirit level.

To summarize reconstruction methods, each frame to be analysed was projected and the centre point of each bird was marked at the mid-point of wing span. The length of each image was measured, and the average was used to find the correct base bisector length. Each centre point was assigned x, y coordinates, and linear, least-squares regressions were used to draw each V leg. Angle a was calculated from the maximum angle of inclination (angle k) and the inclination angle for the frame (angle g , Fig. 8). A point was selected behind the last bird in the longest leg, and the mid-

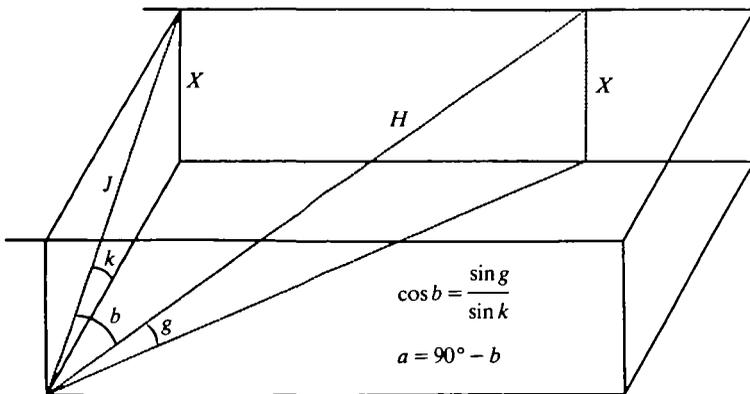


Fig. 8. Method for calculating angle a from measurements of angles g (camera inclination angle) and k (maximum angle of camera inclination). This method assumes a formation flies in a straight line past the perpendicular. H and J represent lines of sight to a formation off and on the perpendicular to the flight path. X is the height of the formation.

point to the apex was marked. A line parallel to the other leg was drawn from this point. The intersection of the base and base bisector (at angle a) was positioned on the parallel line with the base passing through the end-point of the longest leg and the base bisector passing through the apex. (I used tracing paper with two lines forming angle a to do this.) Angle c and the corrected base bisector length were used to find the isosceles leg lengths at the perpendicular. Points not on regression lines were translated there both parallel (for WTS) and perpendicular (for depth) to the base bisector, and the V was transformed using the maximum angle of inclination (angle k) to give the geometry as seen directly overhead (Fig. 4). Distances between adjacent birds along the length of V legs were then used to calculate depth (using cosine of one-half the V angle) and WTS (using sine of one-half the V angle and subtracting a wing span of 1.5 m).

Errors could occur if formations deviated from a straight line. The orientation of bird lengths provided an independent measure of flight direction (Fig. 7). I only analysed films where my calculation of flight direction (the position of the V base bisector) was within 5° of the average orientation of bird lengths. [Bird orientations could vary when individuals made minor adjustments in positions (see Results).]

Additional errors could occur from inaccuracies in measuring inclination angles and/or if perspective distortion did not match the rectangular model (Fig. 3). To assess these, I photographed a 50° model V in the laboratory. The V was moved in a straight line to achieve various inclination angles. Table 1 gives comparisons of measured and calculated values for angle a . The increasing error as angle a decreased may be partly from convergence of the flight path with the horizon. Thus a trapezoid may be a better representation than a rectangle for small values of a , but the rectangular model serves as a simple approximation close to the perpendicular. I limited analysis to values of a greater than 50° . I also limited analysis to geese formations which reached a maximum inclination of at least 40° , since measurement errors have less impact on angle reconstructions as inclination angles increase (Gould & Heppner, 1974).

I filmed Canada geese formations at Montezuma National Wildlife Refuge, Seneca Falls, NY during the migration periods in autumn 1985 and spring 1986. I present results for eight formations which met the straight flight criterion. Six of these

Table 1. Comparison of measured and calculated values for angle a from photographs of a 50° model V

Measured	Calculated	Difference
90°	90°	0°
82°	81°	1°
78°	80°	-2°
73°	74.5°	-1.5°
68°	67.5°	0.5°
65°	61°	4°
54°	46°	8°
38°	22.5°	15.5°

(formations 1–6) did not stop at the refuge; two (formations 7 and 8) were for birds making local movements near the refuge. The number of birds in formations varied from 5 to 16. In most cases I could not keep all the birds in view as they passed the perpendicular, so analysis was for the first 3–6 birds in each leg. The quality of film images varied because of periodic slight movements of the camera necessary to track the geese, and I selected for analysis frames that gave the best resolution of bird images at 1- to 2-s intervals. Times for the eight formations varied from 3.7 to 15.7 s and totalled 70.4 s. 451 wing spacings and depths were measured for 55 birds across the eight formations over this time.

RESULTS

Variation in wing tip spacing

The distribution of all WTS showed a positive skew (Fig. 9), so I used the median as a measure of central tendency and non-parametric statistics to compare distributions. The median of all WTS was -19.8 cm (Table 2). The distribution is similar to one reported for 50 formations of Canada geese from analysis of film images taken at the perpendicular to the camera (Badgerow, 1985). Although the median spacing was within a few centimetres of the predicted optimum, there was considerable variation, ranging from -130 cm overlap to about two wing spans (289 cm) gap (Fig. 9; Table 2). With the assumptions involved for the distribution in Fig. 2, the extremes would result in variations in savings for induced power from the maximum down to negative values at overlap and down to about 2% at gap. In part this was a consequence of variation between formations (Table 2; Kruskal–Wallis analysis of variance, $H = 39.6$, $P < 0.001$).

The variation in WTS was also a consequence of differences in spacings maintained by individuals within formations. The WTS of representative birds is shown as a function of time in Fig. 10. Some individuals ‘tracked’ the optimum with relative

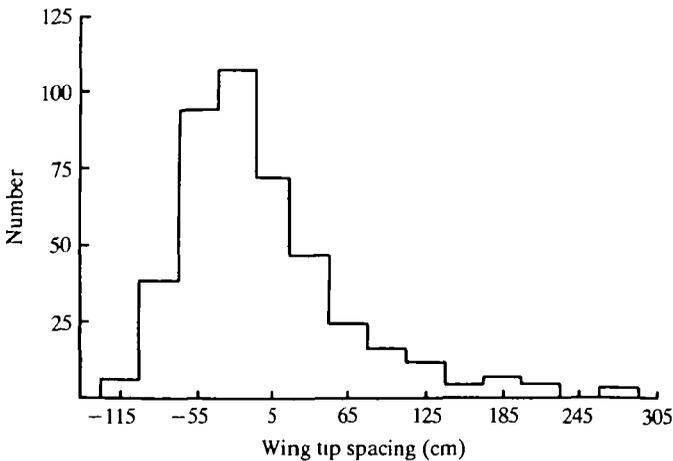


Fig. 9. Frequency distribution of wing tip spacings for 55 geese from eight formations.

Table 2. Median and range for wing tip spacing (WTS, in cm) for eight geese formations

Formation	N	Range	Median
1	81	-100 to 289	-18.9
2	109	-91 to 129	-16.6
3	30	-73 to 134	-0.5
4	36	-84 to 54	-37.5
5	60	-128 to 194	-44.4
6	62	-105 to 189	12.0
7	30	-106 to 84	-35.5
8	43	-98 to 109	-24.4
Total	451	-128 to 289	-19.8

precision most of the time (Fig. 10A), while other individuals within a formation maintained relatively large WTS (Fig. 10B, bird 3).

Individual differences in WTS were associated with the depth between birds. If geese always positioned themselves at an optimum, then WTS should be independent of depth behind the bird ahead (Badgerow, 1985). Fig. 11 shows median WTS as a function of median depth for the 55 geese. There was a significant positive correlation ($r = 0.69$, $t_{(53)} = 7.045$, $P < 0.001$ for test against a slope of zero). Most geese were clustered at depths between 100 and 500 cm. Six had median depths greater than 500 cm. Geese at large depths accounted for most of the extreme positive spacings in the total distribution of WTS. Those with a depth greater than 500 cm had a median WTS of 54.5 cm, while those with a depth less than 500 cm had a median spacing of -28.2 cm ($P < 0.001$, Mann-Whitney U -test, $Z = -8.71$). Some individuals at relatively large depths closed on the individual ahead and experienced more favourable energy savings (Fig. 10A, bird 2), but others did not (Fig. 10B, bird 3). The six geese with relatively large median depths occurred in five formations, so they were distributed uniformly across formations.

Formations were composed of separate 'clusters' of individuals. Within a formation a string of birds would be located within depths of 1-3 wing spans followed by another string of birds with similar depths but with a relatively large depth to the 'leader' of the second string. A similar pattern has been described by Nachtigall (1970). One formation showed behaviour suggesting that clusters of individuals could behave independently. Part-way through the filming sequence, the second bird in one leg moved to the second position in the other leg. This produced an immediate increase in WTS and depth for the bird which had been trailing it. Within 3 s this bird had followed behind the other. This resulted in an even more dramatic increase in WTS and depth for the bird which had been trailing it. This individual and those trailing it then took a separate path and eventually joined with another V.

Active and passive positioning

This example emphasizes that wing spacing variation depends importantly on the bird ahead. Even when birds maintained depths within a few wing spans, their WTS could change abruptly and unpredictably as the bird ahead changed position. I

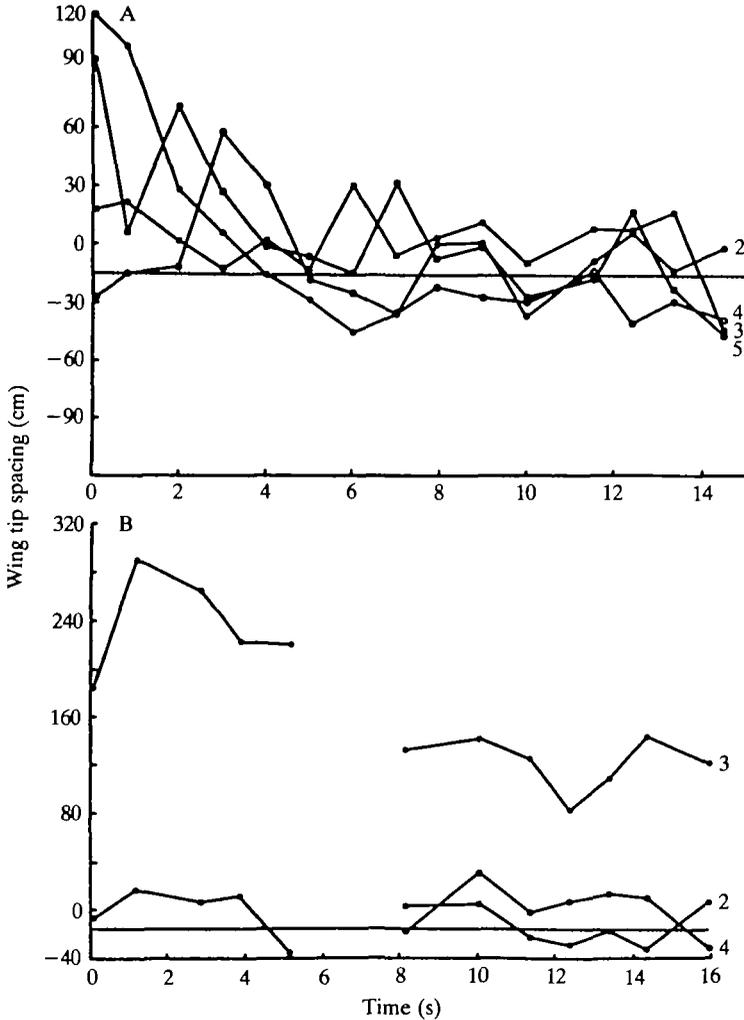


Fig. 10. Individual wing tip spacings (WTS) over time. Each graph presents data for one leg of a V with different symbols for each bird. Numbers to the right of each set of lines give the position of the birds in the V legs. The dashed line is the predicted optimum WTS of -16 cm.

defined a 'passive' change in WTS as one opposite in direction to the change of the bird ahead since any move by the bird ahead would automatically produce the opposite direction change in WTS without any position adjustment by the trailing bird. An 'active' change in WTS was defined as a change in the same direction as the bird ahead since this would not be predicted unless a trailing bird adjusted its position.

Table 3 summarizes the average proportions of 'active' adjustments of WTS for the eight formations. For all formations slightly more than half the changes in WTS were 'active', and there was a four-fold variation between formations in the average proportion of 'active' adjustments. About 38% of the changes in WTS were 'active'

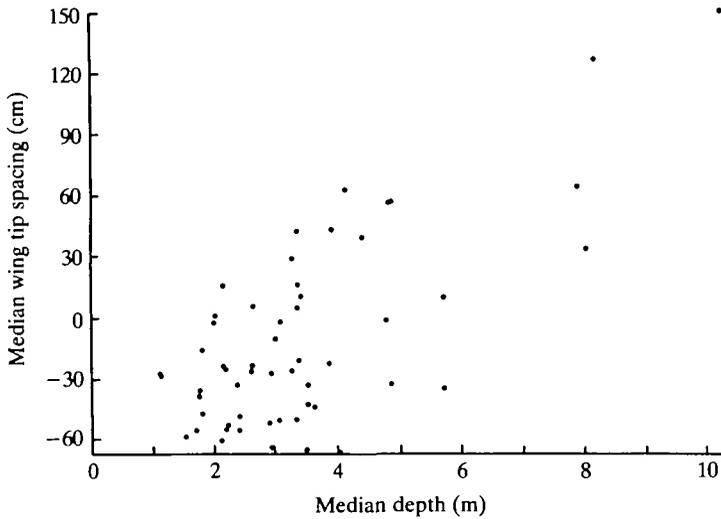


Fig. 11. Median wing tip spacing as a function of median depth. Data for 55 geese from eight formations.

adjustments towards the predicted optimum (Table 3). This suggests that much of the variation in WTS is a consequence of unpredictable moves by birds ahead which then require an adjustment of position in response.

'Active' adjustments of WTS involved changing flight direction relative to the bird ahead. In most cases this occurred with little change in depth. There was considerably less variation in depth within than between individuals. The average for all depths was 359.7 cm with a standard deviation of ± 218.5 cm. The average depth for individuals ranged from 123.9 ± 42.2 to 1188.7 ± 377.4 cm. The average standard deviation for depth within individuals was ± 71.7 cm. Thus, most birds adjusted WTS without the costs associated with increased flight speed that are required to decrease depth.

Table 3. Average percentages of 'active' adjustments of wing tip spacing (WTS) and average percentages of 'active' adjustments of WTS towards the optimum for eight geese formations

Formation	N	% 'Active'	% 'Active' (towards optimum)
1	48	62.5	37.2
2	67	53.8	31.8
3	45	49.9	25.0
4	20	65.0	40.0
5	16	81.2	68.7
6	35	42.9	40.0
7	16	18.7	12.5
8	22	70.5	51.7

Rate of change of wing tip spacing

If the birds are sensitive to energy savings, then variation in WTS could be limited by the way they respond when they are displaced. Table 4 summarizes results for linear regressions between rate of change of WTS and distance from the optimum for changes in position towards the optimum from overlap and gap positions (defined relative to the predicted -16 cm optimum). I analysed data for formations with at least five position changes in an appropriate direction. The first entry for each formation in Table 4 is for all position changes towards the optimum, and a second entry is for 'active' changes towards the optimum. Four of the eight formations had linear regressions with significant slopes for movements back towards the optimum from overlap positions; only two of the eight had significant slopes for movements back towards the optimum from gap positions. Regressions for 'active' changes in WTS towards the optimum improved correlations for five of the six formations for movements from overlap positions, but only three of the six were significant in slope (Table 4).

Three formations (1, 2, 8) showed control of WTS from significant regression slopes for 'active' adjustments, while three formations (3, 6, 7) showed no evidence for control by any regression criterion (Table 4). The formations showing control had a median WTS of -17.8 cm, while those showing no control had a median WTS of -1.0 cm (Mann-Whitney U -test, $Z = -2.23$, $P = 0.024$). The difference may reflect the distribution of savings (Fig. 2) and the ability to control position. If savings decrease over a greater distance towards gaps, birds with little control over

Table 4. *Results of linear regressions for rate of change of wing tip spacing versus distance from the optimum for movements towards the optimum from overlap and gap positions*

Formation	N	Overlap		N	Gap	
		r^2	P		r^2	P
1	18	0.07	0.30	14	0.02	0.65
	10	0.46	0.03			
2	29	0.16	0.03	27	0.36	0.001
	10	0.51	0.02			
3	8	0.27	0.18	8	0.005	0.64
	6	0.43	0.16			
4	12	0.34	0.04	5	0.02	0.67
	6	0.07	0.62			
5	13	0.05	0.50	9	0.68	0.006
	7	0.49	0.08			
6	11	0.28	0.09	21	0.08	0.21
7	7	0.45	0.10	9	0.02	0.69
	8	0.69	0.01			

First entries for each formation are for all moves towards the optimum.

A second entry is for 'active' moves (see text for definition).

All probabilities are from t -tests comparing slopes with a slope of zero.

WTS could still achieve some savings with spacings distributed in this direction. Birds with the ability to control WTS may show WTS more towards overlap, because distances from the optimum are smaller and position adjustments would result in more time spent near an optimum (Badgerow & Hainsworth, 1981).

Depth and the lead bird

Theoretically, the lead bird could experience the same energy savings as other members of a formation (Lissaman & Schollenberger, 1970; Hummel, 1983). In a line-abreast formation the middle bird would have greater savings than the end birds (by a factor of 2 in large formations). Positioning the lead bird ahead of, but close to, trailing neighbours would equalize its savings if it is placed so that the bound vortex about the wings of trailers provides a lift equal to that for other birds. A formation giving equalized savings among birds could be a 'swept V' with the depth from the leader to its neighbours less than the depth between other birds (Lissaman & Schollenberger, 1970; Hummel, 1983).

I tested for this by comparing depths between lead birds and their neighbours with depths between all other birds. The median depth between lead and second birds was 328.1 cm, while the median depth between all other birds was 304.9 cm (Mann-Whitney *U*-test, $Z = -2.06$, $P = 0.037$). Since the result is opposite to that predicted, it appears that lead birds in these formations are too far forward for equalized savings with a 'swept V'.

Most birds were within 1–3 wing spans behind the bird ahead. A trailing wing tip vortex becomes fully formed within 1–2 wing span depths (Higdon & Corrsin, 1978), and this may be important in determining depth for most geese. A 'swept V' produced by positioning trailers close to a lead bird may not be utilized because of different circulation patterns close to a wing. The depth of most geese close to where vortices are formed would also be important for maximizing induced power savings if vorticity dissipates over distance.

Hummel (1978) calculated lower savings for lead birds in V formations with the same depth between birds (7% for the leader *vs* 30% for trailing birds at optimum spacing). If this is the case, then savings for lead birds may be similar to savings for those trailing individuals where depths are relatively large and savings are relatively low.

DISCUSSION

All geese except those occasionally at extreme overlap of WTS save some energy by flying in formation, but the amount depends on the ability of individuals to fly with precision. Some formations showed significantly different WTS from others, and this may be due to flight conditions at different times. For example, windy conditions during flight may make precision flight more difficult by inducing additional unpredictable position moves. I filmed formations under relatively benign weather conditions to maximize the time for straight flight paths, but local differences in turbulence may have contributed to variation between formations. It would be

interesting to compare the flight precision of these geese with those flying under more adverse conditions. My observations of flight under windy conditions suggest frequent changes in direction, propagated 'oscillations' along the lengths of V legs, and a more frequent break-up and reformation of Vs.

Most geese realized appreciable savings from formation flight measured using the model of Lissaman & Schollenberger (1970) to estimate induced power savings. The median WTS of -19.8 cm corresponded to a saving of about 36% compared with solo flight (Fig. 2). This is about half the predicted maximum possible for birds in an 'infinite' formation with spacing at the optimum. Geese in formations showing control of WTS based on rate of change of WTS adjustments achieved a median spacing very close to the predicted optimum.

Savings are for induced power. The extent to which savings occur in total costs for flight will depend on flight speed and the sum of power for induced, profile and parasite drag (Rayner, 1979).

Savings were enhanced by periodic 'active' adjustments in position with individuals in some formations responding to displacement from the optimum by adjusting position proportionally to the extent of the displacement. Adjustments towards the optimum were more common for birds displaced in the overlap region where savings may decrease rapidly with distance (Fig. 2; Badgerow & Hainsworth, 1981). Even though birds in some formations did not respond to displacement from the optimum in a proportional manner, their maintenance of WTS more towards the gap direction may represent a response to achieve some savings when ability to control WTS is less.

'Leaders' obtained relatively low savings. They included birds at the apex of Vs and individuals positioned at relatively large depths from the bird ahead. There were six of the latter and eight of the former in a total of 63 birds, so 'leaders' constituted 22%. Their function is unclear. Perhaps they serve a social or group orientation function (Hamilton, 1967). Their behaviour is intriguing since it appears altruistic. Savings for a bird at the apex could be enhanced if a V became 'swept', and this pattern occurred in some formations (Hummel, 1983). It would be interesting to study the situations where this geometry becomes frequent.

The interpretation of induced power savings is based on the model assuming a steady wing (Lissaman & Schollenberger, 1970). By inference, the results suggest that the model applies to the flight of geese, but variation in vortices from wing movements should not be ignored. The frequent occurrence of WTS less than the predicted optimum may be related to movements of wings which would reduce effective span during parts of a beat cycle. Although the movement of the wings is reduced at high flight speeds, it produces an oscillation in trailing tip vortices (Rayner, 1985a; Rayner *et al.* 1986). If the geese are sensitive to this variation, then the position of the wings of trailing birds may be a function of the wing position of the bird ahead and the depth between the birds. Reports of a lack of synchrony in wing beat frequencies for geese in formations suggest it may be difficult for the birds to utilize variation in vortices due to wing movements (Berger, 1972). However, it would be interesting to obtain information on wing phase relationships for

formations where it is known that birds can control wing positions close to an 'optimum'.

Formation flight is among an impressive series of characteristic modes of locomotion which are thought to represent adaptations for saving energy. These include 'intermittent' flight in birds (Rayner, 1977, 1985*b*), 'burst' swimming in fish (Videler & Weihs, 1982), 'ram' gill ventilation in striped bass and bluefish (Freadman, 1981), 'running' behaviour of dolphins (Au & Weihs, 1980), use of ground effect by 'skimmers' (Withers & Timko, 1977), 'dynamic station keeping' by kestrels (Videler, Weihs & Daan, 1983), 'sweeping' flight by albatrosses (Wilson, 1975), 'queue' movements by spiny lobsters (Bill & Hernnkind, 1976) and salps (Bone & Trueman, 1983) and 'schooling' in fish (Weihs, 1973).

Models of these types of behaviour have been criticized for the assumption that organisms reflect simple engineering models as 'optimal' or perfect solutions to specific problems of survival (e.g. the 'adaptationist programme' of Gould & Lewontin, 1979). But the purpose of optimality models is not to assert that organisms are perfect; rather, they serve to generate hypotheses for testing. Models must be modified whenever variation in performance is other than a predicted optimum. There has probably been strong selection for economy in flight energy expenditure by geese, yet it is clear that other constraints influence performance so only some individuals behave 'optimally' and only some of the time. Other tests demonstrating performance variation in locomotion have led to experiments on multiple functions for schooling in fish (Abrahams & Colgan, 1985), integration of costs and benefit of movement to provide criteria for movement speeds (Pyke, 1981) and hypotheses for constraints on muscle efficiency to explain the full range of use of bounding and undulating flight by birds (Rayner, 1985*b*). Understanding how adaptations are structured is likely to benefit from further tests to explore why individuals vary in performance.

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