

ENERGY SAVINGS IN FORMATION FLIGHT OF PINK-FOOTED GEESE

C. J. CUTTS* AND J. R. SPEAKMAN

*Department of Zoology, Aberdeen University, Tillydrone Avenue, Aberdeen, AB9 2TN,
Scotland*

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Summary

Fifty-four skeins of pink-footed geese (*Anser brachyrhynchus*) were photographed from directly underneath to eliminate the effects of perspective distortion, and the wing-tip spacings (the distance between adjacent birds' wing tips perpendicular to the flight path at maximum wingspan) and depths (the distance between adjacent birds' body centres parallel to the flight path) were measured at the same time as local wind speeds. The photographs were used to test for savings in induced power from wing positioning relative to the predicted positions of vortices generated by other wings, using a theoretical model. The mean wing-tip spacing corresponded to a saving in induced power of 14%, less than one-third of the maximum possible. The saving in total power might be as low as 2.4%. The high variation in wing-tip spacing suggests that pink-footed geese found difficulty maintaining position and thus adopted a strategy of flying outboard of the optimal position that maximises savings. This may minimise the risk of straying into a zone where savings are negative. There was a significant correlation between depth and wing-tip spacing, supporting an alternative communication hypothesis, whereby the birds position themselves to obtain maximum information on their neighbour's position. In high winds, there was little change in wing-tip spacing variation but a decrease in depth variation, suggesting a shift towards more regularly spaced skeins.

Introduction

A striking feature of goose flight is the frequent adoption of a V-shaped flight formation. Two hypotheses have been advanced to explain the use of this flight formation. First, it may be an adaptation for reducing the energy costs of flight (Lissaman and Shollenberger, 1970; Badgerow and Hainsworth, 1981; Hainsworth, 1987), which are known to be great for flying vertebrates (Tucker, 1973; Rothe *et al.* 1987; Speakman and Racey, 1991). Alternatively, the V may reflect a mechanism by which birds avoid collisions with each other and stay in visual contact (Gould and Heppner, 1974; Williams *et al.* 1976).

*Present address: Department of Zoology, Glasgow University, Glasgow, G12 8QQ, Scotland.

The pressure difference between the top and bottom of a bird's wing, which provides lift, cannot be sustained beyond the wing tips since there is no surface to separate the two pressure regions. Consequently, the high-pressure air under the wing flows around the tip and inward across the dorsal wing surface. This latter flow forms a sheet of turbulent air shedding from the trailing edge into the bird's wake (Higdon and Corrsin, 1978). This planar vortex sheet rolls up into two concentrated tubular vortices, one issuing from each wing tip (Higdon and Corrsin, 1978; Rayner, 1979; Hummel, 1983).

The vortices, which are slightly inboard of the wing tips, produce large regions of upwash outboard of the wing and a region of downwash more centrally. The regions of upwash may contribute to the lift of a following bird, thus reducing its requirement for induced power (Pennycuik, 1969). The potential savings depend on wing-tip spacing (Lissaman and Shollenberger, 1970), where the wing-tip spacing of two birds is defined as the distance between the centres of the two bird bodies minus their mean maximum wingspan. As wing-tip spacing decreases, the induced power required in formation flight also decreases because the following bird is flying in a progressively stronger upwash from the shed vortices of its neighbour. Beyond a critical negative wing-tip spacing, however, the following bird starts to fly in the central downwash and experiences an increase in costs, or a negative saving. Hence, there is an optimal wing-tip spacing (WTS_{opt}) which maximises the reduction in induced power requirements. This theory is derived for fixed wings but can be applied to flapping flight (Hummel, 1978).

The horizontal distance between the tubular vortex centres (d_v) behind a fixed wing is:

$$d_v = (\pi/4)b, \quad (1)$$

where b is wing span (Higdon and Corrsin, 1978; Hummel, 1983; Hainsworth, 1987, 1988). However, in a more rigorous model, Hummel and Beukenberg (1989) derive the distance between the vortex centres as $0.89b$, rather than $(\pi/4)b (=0.78b)$. Since 0.89 is less than 1.0 and the regions of upwash are outboard of the vortex centres, the optimum wing-tip spacing that maximises induced power savings (WTS_{opt}) will be a negative value:

$$WTS_{\text{opt}} = 0.5b(1 - 0.89). \quad (2)$$

A negative wing-tip spacing can only be achieved by overlapping wing tips, which is achieved in the V formation. In theory, at the optimal wing-tip spacing (WTS_{opt}), formation flight may require only 50–60 % of the induced power of solo flight (Lissaman and Shollenberger, 1970; Hainsworth, 1987). In addition to wing-tip spacing, birds may affect their savings by varying the distance they fly behind the bird in front. The vortex sheet behind a fixed wing in steady level flight rolls up to form two concentrated vortices within two chord lengths (maximum wing width) of the wing (Rayner, 1979). At progressively increasing distances beyond the point where the tubular vortices first form, their rotational vorticity decreases (this distance is perpendicular to wing-tip spacing and is called depth) and, since the vortices are less concentrated in front of the roll-up point, they will provide less assistance. In theory, the effect of depth is insignificant after this point (Hummel, 1978). However, in practice, the exact location of the vortex will vary as a result of wind and thus the predictability of the position will decline. Therefore, the roll-up point represents an optimum spacing for depth. However, the break-up and reduction

in vortex strength with depth are poorly understood (Badgerow and Hainsworth, 1981; Hainsworth, 1987, 1988; Badgerow, 1988). If a bird's depth relative to the bird in front increases, the energy saving hypothesis predicts that there should be no parallel increase in the wing-tip spacing.

The prediction of optimal positioning to maximise energy savings can be compared with the alternative hypothesis that the spacing in a V is for orientation and communication (Gould and Heppner, 1974; Williams *et al.* 1976). This latter hypothesis predicts that wing-tip spacing and depth should be positively correlated to maintain a constant angle between the geese. This may provide an efficient method for communication of flight path and velocity between birds (Badgerow, 1988).

In the present study, we observed pink-footed geese (*Anser brachyrhynchus*) to test whether the positions of birds in the formations were such that wing-tip spacing and depth matched the predictions of aerodynamic theory for achieving maximum energy conservation or matched predictions of the communication hypothesis. We also assessed whether adverse wind conditions affected the ability of geese to maintain formation.

Materials and methods

Goose skeins were photographed from directly below with a tripod-mounted twin lens reflex camera (Mamiya C330) with an 80 mm lens. A spirit level was used to ensure that the camera was pointing vertically at all times. This allowed analysis of the photographs for wing-tip spacing and depth without correction for perspective distortion. Height between birds could therefore not be measured, but Hummel and Beukenberg (1989) have shown that height does not greatly affect the optimum wing-tip spacing. A fast shutter speed of 1/125 s and fast black and white film (400 ASA, Tri-X, Kodak) was used for image clarity.

All photographs were taken between 15 October and 3 November 1991, during the hours directly after dawn (07:00 h to 09:00 h) and before dusk (16:00 h to 18:00 h), when goose skeins were at maximum numbers. When photographing the skein, the flight direction was noted, along with wind speed and direction. Mean wind speeds were estimated with the Beaufort scale (Berry *et al.* 1945), which gives minimum and maximum wind speed values at 10 m height. Mean wind speeds appropriate for each photograph were calculated by taking the average of the minimum and maximum values of the range (approximately 2.5 m s^{-1}) provided by the Beaufort scale.

Fifty-four skeins of pink-footed geese were photographed at the RSPB reserve Loch of Strathbeg, 58 km north of Aberdeen, Scotland ($57^{\circ}37' \text{ N}$, $1^{\circ}50' \text{ W}$). The camera was set up on a road intersecting the flight path, 625 m south-west of the main roost site (OS 1:25 000 series; NK 05/15; grid reference: 0558). As the road bisected the flight path at 90° , this allowed the camera to be moved between positions along the width of the flight path. There was a large degree of variability between flight lines within the flight path, although generally the pink-footed geese flew to and from the south-west of the roost.

To measure the wing-tip spacings and depths from the photographs, a standard scale measure was taken from a sample of 14 dead birds. Bill-to-tail length was the measure used to scale the photographs. Bill-to-tail length may potentially vary as a result of

stretching and contraction in the neck during flight. Two measurements were taken of each goose: one with its neck extended but relaxed, and another with its neck stretched to maximum length. The mean of these two values was used as the mean bill-to-tail length for each individual goose, and the mean of these values was used as the measure to evaluate scale in the photographic analysis. Wing span (b) was also measured in the same sample of birds by spreading their wings out sideways to their fullest extent. Span was used to predict the optimum wing-tip spacing (WTS_{opt}) and also to calculate the observed wing-tip spacing from the photographs.

Where the skein consisted of fewer than eight birds, we measured all the bill-to-tail lengths. Otherwise we measured eight bill-to-tail lengths from each photograph, and the mean of this sample was used as the scale for that particular photograph. The wing-tip spacing and depth could be evaluated directly from the photographs by measuring them on the photographs and estimating them as functions of the standard bill-to-tail length for that photograph.

The large-format (56 mm×56 mm) negatives were printed onto Ilford A5 squared paper (15 cm×15 cm). Measurements were taken from the prints with vernier callipers (accurate to 0.1 mm). The implications of this accuracy for the error in estimated wing-tip spacing and depth varied from picture to picture. The higher a skein flew, the less precise the estimates became, because bill-to-tail length on the film decreased with increasing height, making the scale larger, hence 0.1 mm on a photograph represented a correspondingly larger actual distance. Enlarging the negatives further, however, induced other errors since the images became progressively less defined. On average, we estimated that 0.1 mm was equivalent to 1.7 cm.

Wing-tip spacing was measured by drawing a line back from a goose's body centre along the direction of travel and measuring the distance between the line and the following goose's body centre perpendicular to the direction of travel. This figure was converted to wing-tip spacing by subtracting the mean wingspan from the sample of dead birds. Depth was measured as the distance between adjacent body centres parallel to the direction of travel. The body centre was defined as midway between the bill and tail and midway along the wingspan. The range of skein sizes used was 3–27 geese (mean 8.4 ± 0.7 , \pm S.E.M.; S.D.=5.2).

Results

Measurements of dead birds

Fourteen dead birds were measured. The mean wing span (b) was 108.5 ± 1.5 cm (S.D. 5.4 cm). Mean bill-to-tail length was 66.5 ± 0.3 cm (S.D. 1.1 cm). The mean wing chord was 23.1 ± 0.8 cm (S.D. 3.0 cm).

Derivation of prediction of WTS_{opt} and optimal depth to maximise energy savings

We used the estimated span from the sample of dead birds to calculate the optimal wing-tip spacing (WTS_{opt}) using equation 2. Using Hummel and Beukenberg's (1989) model, we estimated the vortex filaments behind a pink-footed goose to be 96.6 ± 1.1 cm apart. Therefore, the optimum wing-tip spacing (WTS_{opt}) was predicted to be

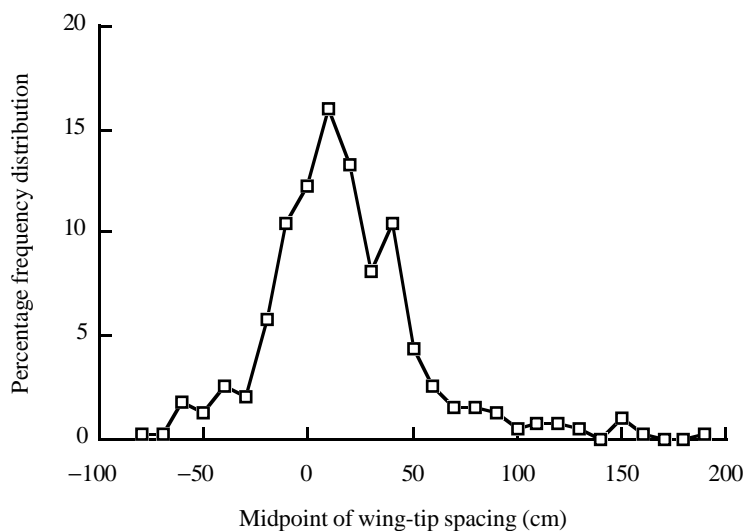


Fig. 1. The distribution of 393 individual wing-tip spacings from 54 skeins of pink-footed geese. The predicted optimal wing-tip spacing which maximised induced energy savings was -6.0 cm.

-6.0 ± 1.1 cm. Given the mean wing chord of the dead birds, we also estimated the optimal depth to maximise energy savings ($2 \times$ wing chord). To maximise energy savings, we thus predicted that birds should fly at a depth of 46.2 ± 1.6 cm.

Measurements of wing-tip spacing

Three hundred and ninety-three individual wing-tip spacings were measured across 54 skeins. The distribution of observed wing-tip spacings pooled across all skeins (Fig. 1) was compared with the predicted wing-tip spacing (WTS_{opt}) maximising energy savings. The distribution of wing-tip spacings was approximately normal. The mean wing-tip spacing was $+16.9 \pm 1.9$ cm (s.d. 38.4 cm).

The wing-tip spacing index, R , is:

$$R = b_{EFF} / (b_{ACT} + WTS) \quad (3)$$

(Badgerow and Hainsworth, 1981), where b_{EFF} is the effective wingspan of 102.5 cm ($b_{ACT} - WTS_{opt}$), b_{ACT} is the actual wingspan of 108.5 cm and WTS is the wing-tip spacing. $R=1$ when wing-tip spacing is optimal.

As induced drag is reduced, energy savings increase by a factor of $1/e$, where e is a measure of energy savings available through formation flight. Percentage energy savings can be derived from this relationship and can be plotted against R , with the maximum saving when $R=1$ (Lissaman and Shollenberger, 1970; Badgerow and Hainsworth, 1981).

A theoretical maximum saving of 51% is possible for an individual in a V formation of eight geese when they fly at optimal wing-tip spacing (Badgerow and Hainsworth, 1981). For the mean wing-tip spacing of $+16.9$ cm observed here, the wing-tip spacing index is 0.8. Owing to the asymmetrical distribution of savings about the optimal wing-tip spacing

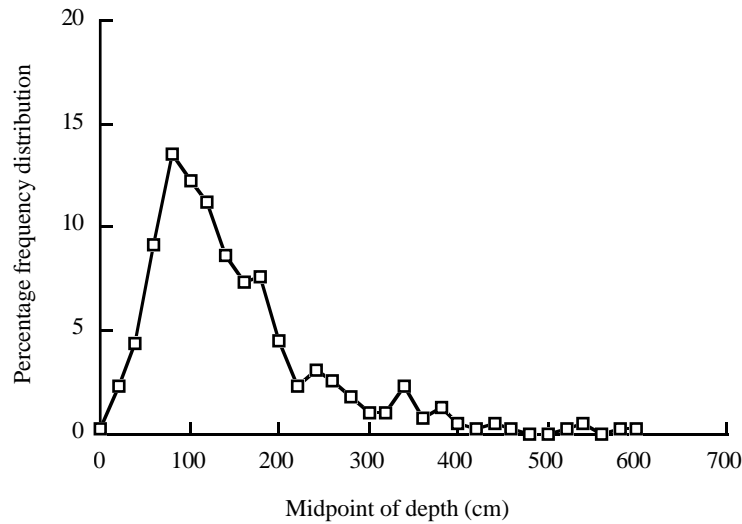


Fig. 2. The distribution of 393 individual depths from 54 skeins of pink-footed geese. The predicted optimal depth which maximised induced energy savings was 46.2 cm.

(WTS_{opt}) (Hainsworth, 1987), an R value of 0.8 corresponds to a theoretical saving of approximately 14%.

The observed wing-tip spacings ranged from -89.8 to $+188.7$ cm, a range of almost two wing spans. This range includes energy losses (negative savings) at the point where the goose's centre lies in the vortex and savings of 51% at the optimal spacing. 75% of the geese had positive wing-tip spacings.

Measurements of depth

Three hundred and ninety-three individual depths were measured across 54 skeins. The distribution pooled across all skeins was positively skewed (Fig. 2). The mean depth was 150.3 ± 4.9 cm (s.d. 97.7 cm) but, owing to the skewedness of the graph, the mode (80 ± 10 cm) was taken as the measure of central tendency. The minimum and maximum values were 5.5 and 596.3 cm respectively. Only 2.5% of the observed depths were less than the depth of 46 cm, in which zone no vortex filaments are predicted to be present. Theoretically, the lead birds could obtain an advantage from a bound vortex about the wings of their two trailing birds, but presumably this would only be useful when depth is small. However, there was no significant difference between depth for the lead birds in each skein and the depths of the other birds.

Relationship between wing-tip spacing and depth

There was a significant relationship between the wing-tip spacing and depth ($r=0.1$; $r^2=1.8$; $F=7.0$; $P=0.01$; d.f.=392) (Fig. 3). The prediction from the communication hypothesis that there should be a positive relationship between wing-tip spacing and depth was therefore supported. However, the low value of r^2 reflects the fact that this adjustment was not very precise and the ability of the geese to maintain close position was very poor.

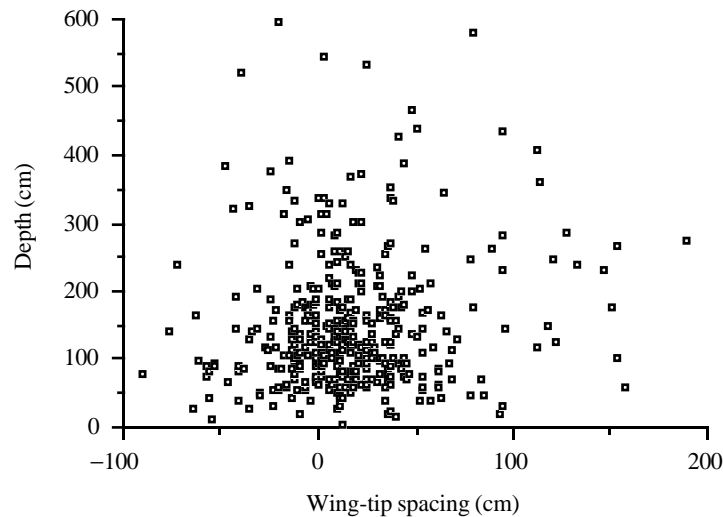


Fig. 3. The relationship between wing-tip spacing and depth from 393 paired wing-tip spacing and depth values from 54 skeins of pink-footed geese.

Effects of wind

When birds fly in high winds they may have difficulty maintaining their position relative to the predicted optima (WTS_{opt} and depth). This inability may manifest itself in two ways. First, birds may become more conservative in their spacings and depths, choosing a more positive spacing than the optima. This strategy would result in lower savings but would minimise the risk of being blown into the downwash or vortex sheet area and experiencing no saving or a negative saving. Second, the variation (s.d.) in spacing or depth may increase with wind speed as each individual strives with increasing difficulty to maintain position.

There was no significant relationship between mean wind speed and mean wing-tip spacing of a skein ($r=0.2$; $N=54$). There was also no significant relationship between the standard deviation of wing-tip spacing and speed ($r=0.2$; $r^2=5.5$; $F=3.0$; $P=0.09$; d.f.=53) (Fig. 4). However, both relationships approached significance.

There was no significant relationship between mean wind speed and mean depth ($r=0.02$; $N=54$). However, standard deviation of depth was significantly related to the wind speed ($r=-0.3$; $r^2=10.0$; $F=5.8$; $P=0.02$; d.f.=53) (Fig. 5). The direction of this relationship was, however, the opposite of that predicted. Thus, at high wind speeds, the birds became more regular in their depth spacing.

Discussion

Wing-tip spacing

All the observed geese, except those at extreme wing-tip overlap (3% of the total) saved some energy by formation flying. The saving of 14% of induced power represented by the mean observed spacing was well below the theoretical maximum saving possible

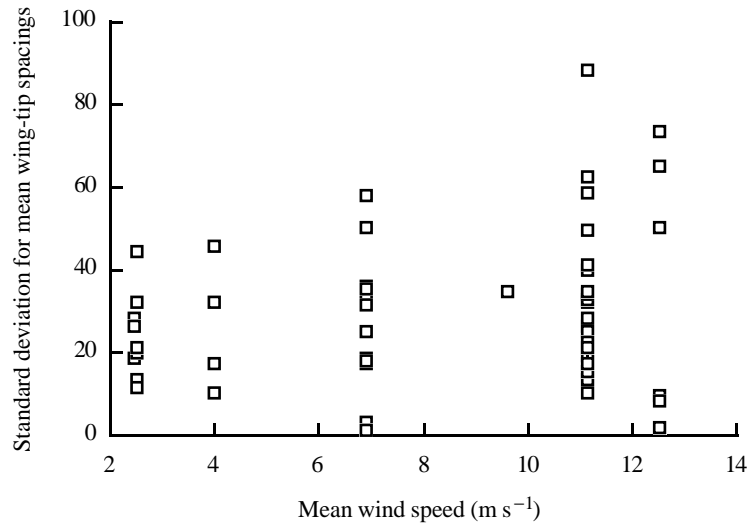


Fig. 4. The relationship between mean local wind speed and the standard deviation for mean wing-tip spacings from 54 skeins of pink-footed geese.

for nine geese in formation of 51 % (Lissaman and Shollenberger, 1970; Badgerow and Hainsworth, 1981). This was due to the predominance of positive spacings.

The distribution of spacings either side of the optimal wing-tip spacing is asymmetrical and quite sharply peaked around the optimum (Hummel and Bock, 1981; Hummel and Beukenberg, 1989), losses being experienced when wing-tip overlap is greater than half a wingspan (Hainsworth, 1987). Because of this asymmetry, it has been predicted that the optimal location to fly, if there is error involved in maintaining spacing, would be in the direction of increased wing-tip spacing, particularly if errors in maintaining spacing ability are large (Badgerow and Hainsworth, 1981). In this way, the geese would minimise the risk of experiencing energy losses. The high variation in wing-tip spacings we observed supports the suggestion that birds find difficulty maintaining their positions and thus a less risky strategy of flying, on average, outboard of the optimal location might be favoured.

Canada geese (*Branta canadensis*) in formation experienced an average saving in induced power of 10 % with a maximum of 35 % (Hainsworth, 1987) because they also had greater wing-tip spacings than the optimum. For Canada geese, Gould and Heppner (1974) reported large negative wing-tip spacings, which they interpreted as evidence against the energy saving hypothesis. However, these latter data have been re-examined and it was suggested that Canada geese actually fly close to the optimum wing-tip spacing and thus appear to be able to maintain narrow variations around the optimum (Badgerow and Hainsworth, 1981).

The extent to which savings occurred in total costs for flight depends on flight speed and thus on the sum of power to provide induced power and power to overcome the profile and parasite drag (Rayner, 1979; Hainsworth, 1987; Pennycuick, 1989). Using the Pennycuick model, for example, a pink-footed goose with a mass of 3 kg has a predicted

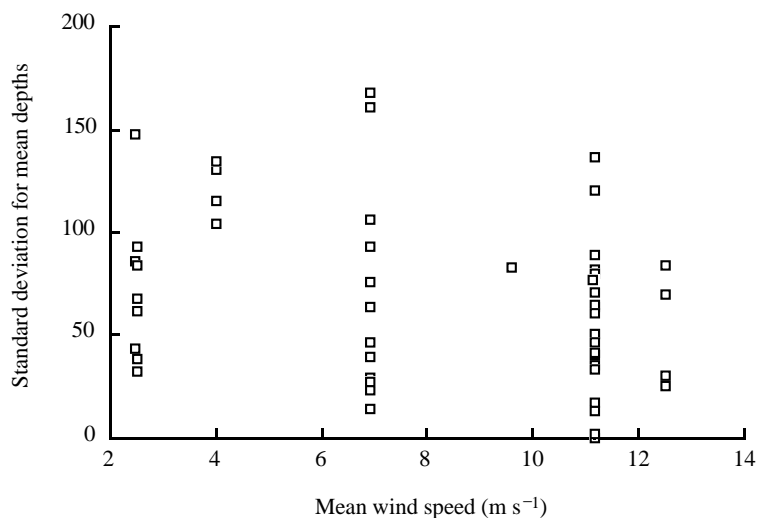


Fig. 5. The relationship between mean local wind speed and the standard deviation for mean depths from 54 skeins of pink-footed geese.

induced power of 29.4 W, a profile power of 47.3 W and a parasite power of 10.0 W when flying at its minimum power velocity of 15.7 m s^{-1} (Pennycuik, 1989). At the maximum range velocity of 25.4 m s^{-1} , the predicted induced power drops to 18.2 W, the predicted profile power remains the same and the predicted parasite power rises to 42.6 W. Savings in formation flight are for induced power only, so at high speeds the total saving is proportionately less. We estimate at the observed mean wing-tip spacing that, if the birds observed here were flying at their maximum range speed, their total saving might amount to only 2.4% of their total predicted flight costs.

Depth

The reduction in strength of vortices behind animals is poorly understood. The intensity of the vortex strength decline behind birds and its break-up are complex processes that are poorly understood for fixed wings and not at all for flapping wings (Higdon and Corrsin, 1978). Intuitively, the optimum distance for depth might be predicted to be where the vortex filaments form: two wing chords behind the goose in front (46.2 cm for pink-footed geese). The modal observed depth of 80 cm was not close to this figure, but may reflect a distance where the vortex is still strong enough to bestow an induced power saving, but not so close that there is any risk of collision or erroneous movement into the zone where tubular vortices have not yet formed.

Relationship between wing-tip spacing and depth

The prediction of the communication hypothesis, namely that wing-tip spacing and depth should be positively related to provide information on position, was supported. Although the adjustment was not precise, there was a significant trend for birds at larger depths to be found at wider wing-tip spacings. Gould and Heppner (1974) interpreted a large negative wing-tip spacing as support for the orientation/communication hypothesis;

however, this interpretation was rejected by Badgerow and Hainsworth (1981). Williams *et al.* (1976) used radar to measure the length and angle of Canada goose formations and found a significant negative relationship between V length and V angle. They suggested that formation flight was probably not the result of a single energetic factor but might have social components as well.

Badgerow (1988) studied 50 skeins of Canada geese; 8 supported the orientation/communication hypothesis, 27 supported the energetic hypothesis, 10 supported both simultaneously and 7 were indeterminate. However, 7 of the 8 formations that supported the communication hypothesis occurred in autumn on local flights. These skeins probably included young on their first migration. The presence of inexperienced geese could have placed a premium on orientation/communication (Badgerow, 1988). This may also be a factor for the pink-footed geese in this study, as it too took place in the autumn, less than a month after they had arrived from their breeding grounds in Iceland.

Effects of wind

We predicted that windy conditions during flight might make precision flight more difficult by inducing both unpredictable bird and vortex positions (see Hainsworth, 1987). However, we found no significant change in wing-tip spacing variation with increasing wind speed, suggesting that in high winds goose skeins maintained similar variation to that on calm days.

The variation of mean depth significantly decreased with increasing wind speed. Little is known about the importance of depth, but in high winds the vortex is likely to break up more rapidly and its location become unpredictable the further back a goose flies; therefore, a shift towards skeins with more regular depths at high wind speeds may compensate for the unpredictability of the vortex locations. The lack of any significant relationship between the standard deviation of wing-tip spacing and wind speed suggests that wind does not have a major effect on optimal positioning.

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