Energetic influence on gull flight strategy selection

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Summary

During non-migratory flight, gulls (Larids) use a wide variety of flight strategies. We investigate the extent to which the energy balance of a bird explains flight strategy selection. We develop a model based on optimal foraging and aerodynamic theories, to calculate the ground speeds and airspeeds at which a gull is expected to flap or soar during foraging flight. The model results are compared with observed flight speeds, directions, and flight strategies of two species of gulls, the black-headed gull Larus ridibundus and the lesser black-backed gull Larus fuscus. The observations were made using a tracking radar over land in The Netherlands.

The model suggests that, especially at combinations of low ground speed (~5–10 m s\(^{-1}\)), high air speed (~20–25 m s\(^{-1}\)) and low ground and air speed, gulls should favor soaring flight. At intermediate ground and air speeds the predicted net energy gain is similar for soaring and flapping. Hence the ratio of flapping to soaring may be higher than for other air and ground speed combinations. This range of speeds is broadest for black-headed gulls. The model results are supported by the observations. For example, flapping is more prevalent at speeds where the predicted net energy gain is similar for both strategies. Interestingly, combinations of air speed and flight speed that, according to the model, would result in a loss of net energy gain, were not observed. Additional factors that may influence flight strategy selection are also briefly discussed.

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Key words: flapping flight, foraging theory, Larus ridibundus, Larus fuscus, soaring.

Introduction

Aerodynamic theory adapted for avian flight (e.g. Tucker, 1975; Pennycuick, 1989; Rayner, 2001) is a tool that has been used to develop and investigate theories in optimal flight behavior of birds (Alerstam and Lindstrom, 1990; Hedenström and Alerstam, 1995; Liechti and Bruderer, 1998; Thomas and Hedenström, 1998; Hedenström, 2002). Some birds may specialize in either powered flapping flight or soaring flight, whereas other birds such as many Larids (gulls), the focus of this study, utilize a wide variety of flight strategies (e.g. Snow and Perrins, 1998). Theoretically, powered flight is energetically more expensive for many species than soaring flight (Hedenström, 1993). Field measurements, for example, have also shown that the energetic cost of soaring by herring gulls (Larus argentatus) is much lower than for flapping (Kanwisher et al., 1978). However, for species that can use different flight strategies, the reasons for selecting a particular flight strategy and the factors determining the flight strategy used remain unclear and have received little attention.

Foraging is an interesting case for studying flight strategy selection because the selection of a particular foraging behavior may strongly influence energy expenditure (Bautista et al., 2001; Weimerskirch et al., 2003). Different currencies in optimal foraging theory can be used to develop and test expectations for foraging behavior of birds (Welham and Ydenberg, 1993; Hedenström and Alerstam, 1995; Bautista et al., 1998). Energy balance, meteorological conditions, or a combination of the two, may be some of the factors that influence flight strategy selection during foraging (Woodcock, 1975; Bautista et al., 2001; Sergio, 2003; Ruxton and Houston, 2004).

In this study we investigate to what extent net energy balances of birds can explain the selection of a soaring or a flapping flight strategy. We develop a static model for flight behavior based on a theoretical framework encompassing optimal foraging and aerodynamic theories. The main hypothesis underlying our model is that the net energy balance over a short time period for an individual bird determines largely whether a bird chooses flapping or soaring flight when foraging. Since flight energetics vary greatly with bird morphology (e.g. Pennycuick, 1989; Norberg, 1990), the model is tested for two gull species of different mass, wing size and shape: the black-headed gull...
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(Larus ridibundus L.) and the larger lesser black-backed gull (Larus fuscus L.). The model is compared to field observations where gull flight behavior has been observed along with measured physical flight parameters. In this study we evaluate whether the results predicted by our model are consistent with the observations. Flight energetics may be strongly influenced by weather conditions. Therefore a model involving variable weather conditions would perhaps be more appropriate to study the proposed system. However, we do not have observations of bird flight nor weather data at a spatio-temporal resolution to calibrate or validate a model of that complexity.

Materials and methods

Observations

As part of a larger study on the influence of meteorological conditions on the flight altitudes of birds (Shamoun-Baranes et al., 2006), the flight speed, direction, altitude and climb rate of black-headed gulls Larus ridibundus L. and the larger lesser black-backed gull Larus fuscus L. were measured. Measurements were conducted during 15 days in the spring and summer of 2000 using a modified HSA MLU-flycatcher tracking radar (Hollandses Signaal Apparaten, Hengelo, The Netherlands) stationed at De Peel military airbase (51°32’N, 5°52’E) in the southeastern region of The Netherlands. The landscape in the area of measurement is flat terrain including low forest and heath. The gulls were tracked within a range of 5 km. Birds were identified visually using a video camera with a 300 mm lens mounted parallel to the tracking radar, as well as with digital wing beat pattern recognition. The flight strategy (flapping, soaring or gliding) was recorded during each track. During observations, soaring and gliding were defined as non-flapping flight with either an increase or decrease in altitude, respectively. In all subsequent analyses, soaring and gliding are treated synonymously and measurements were combined and compared to flapping flight measurements. In total, 54 black-headed gull flight tracks and 97 lesser black-backed gull tracks were recorded. As birds were selected randomly in the course of each day during the 15 days of measurements, we consider each of these tracks to be independent measurements of unique individuals. Mean track duration (± s.d.) was 32±15 s. The mean flight speed (ground speed) was calculated per track and used in the analyses. All observations are of local non-migratory movements. For the purpose of this study, although we do not know the exact aim of the flights of the gulls tracked, we make the assumption (based on time of year and time of day) that gulls are moving to and/or from foraging sites. Tracks of birds that were clearly foraging on aerial prey were excluded from analysis.

Hourly surface wind speed and direction data were collected from the nearest meteorological station at Volkel (51°39’N, 5°42’E). For comparison with optimal foraging predictions we calculated flight air speed and direction from tracked ground speed and direction by using vector summation and subtracting the wind vectors from the flight vectors. The wind speed and direction at the same time and location (horizontal and vertical) of the flight measurements would be optimal; however, they were unavailable. Although the meteorological station is approximately 17 km from the radar location, the surface winds in both areas are comparable considering the landscape properties of the measurement area and the meteorological station (Wieringa, 1986). Furthermore, due to intense vertical mixing in the mixed boundary layer, corresponding to the altitudes at which birds were observed, wind speed and direction are virtually constant over most of the mixed layer (Stull, 1988). Using 12 GMT radiosonde data from De Bilt (52°06’N, 5°11’E), we tested the relationship between winds at 2 m and winds at the 925 mb (1 mb=0.01 Pa) pressure level (approximately 650–850 m) by applying a linear regression analysis of the u component of the wind at 2 m in relation to the u component of wind at 925 mb pressure level. The same analysis was repeated for the v component of wind. $R^2$ values for u and v components were 0.83 and 0.87 for the u and v components respectively ($P<0.001$). Therefore, the surface winds measured at Volkel should be a reasonable estimation of the winds aloft, experienced by the birds. Nevertheless, remotely measured wind that may differ from the wind experienced by the bird will add some uncertainty to the air speed calculations of the gulls.

Predictions from optimal foraging and aerodynamic theory

One of the fitness-related currencies that may be maximized in optimal foraging theory is the net rate of energy gain (Bautista et al., 1998). In a laboratory experiment (Bautista et al., 2001), the switch between walking or flying modes of foraging starlings (Sturnus vulgaris) showed that net rate of energy gain was the currency that best accounted for the choice of foraging mode. Therefore we use the same currency in our study.

All symbols used in the following equations are summarized in Tables 1 and 2. Similar to calculations by other authors (Hedenström and Alerstam, 1995), we calculate the net rate of energy gain when flying between foraging patches as follows:

$$R = \frac{1}{t_p + h} \left( \int_0^{t_p} E_a(t)dt - \int_0^{t} P(t)dt \right),$$

(1)

where R is net rate of energy gain (W), $E_a(t)$ is the energy gain function during foraging (W), $P(t)$ is the associated power of flight (W), $t_p$ is the time of feeding on a patch (s), and $t_i$ is travel time between patches (s).

In optimal foraging studies, energy gain is usually assumed to be a non-linear function relative to the time spent feeding (e.g. Charnov, 1976; Tome, 1988; McNamara and Houston, 1997). However, little is known about the precise shape of $E_a(t)$ for a given species, the results for the ruddy duck (Oxyura jamaicensis) (Tome, 1988) and ring-billed gull (Larus delawarensis) (Welham and Ydenberg, 1988) being notable exceptions. In our study, there is little reason to adopt a complex form for the net energy gain function since we compare the net energy gain for a single bird species when flapping or soaring. Only $t_i$ and $P(t)$ in Eqn 1 affect net energy
gain of a species \((t_p \text{ and } E_n \text{ do not make a difference})\). Moreover, we adopt a value for \(t_p\) that can, within the range of observed values, be adjusted so that a range of values can be obtained for the integral

\[
\int_{0}^{t_p} E_n(t) \, dt.
\]

We can therefore simplify our analysis without loss of generality by replacing \(E_n(t)\) with a constant \(E_n\), so that

\[
\int_{0}^{t_p} E_n(t) \, dt
\]

simplifies to \(E_n t_p\).

Power of flight \(P(t)\) is a nonlinear function that depends on a bird’s flight strategy, a number of biometric parameters and wind conditions. Although wind conditions can vary in space and time we assume \(P(t)\) to be constant for a particular flight between two patches. The most important reason for this simplification is that we consider the travel time and distance between patches to be relatively short in relation to the heterogeneity of the wind field. In addition, we are only able to observe flight behavior (height, speed, direction, and flapping or soaring flight) over a very limited part of a flight track – hence it is practically impossible to define the full power for flight between two food patches. Hence

\[
\int_{0}^{t} P(t) \, dt
\]

simplifies to \(P t\). When assuming \(P\) to be constant over a flight track, we also assume a constant ground speed for the bird.

Combining this with a fixed distance between food patches, travel time \(t\) can be calculated by \(D/V_g\), where \(D\) is the distance (m) between food patches and \(V_g\) (m s\(^{-1}\)) is ground speed of the bird.

Eqn 1 can now be rewritten as:

\[
R = \frac{E_n t_p}{t_p + t} = \frac{P t}{t_p + t}.
\]  
(2)

For a schematic representation of Eqn 1 and 2, see Fig. 1. In our study we will keep \(E_n\), \(t_p\) and \(D\) constant, while varying \(P\) and \(V_g\).

Based on aerodynamic theory for avian flight, as formulated by Pennycuick (Pennycuick, 1989), we parameterize \(P\) as a function of air speed and/or basal metabolic rate, depending on the flight strategy used. The mechanical power for flapping flight \(P_f\) is a function of air speed \((V_a)\) and the summation of profile power \((P_{\text{pro}})\), parasite power \((P_{\text{par}})\) and induced power \((P_{\text{ind}})\), Eqn 3:

\[
P_f = P_{\text{pro}} + P_{\text{par}} + P_{\text{ind}} = \alpha + \frac{\beta}{V_a} + \gamma \cdot V_a^3.
\]  
(3)

(see Appendix in supplementary material for the full formulation and all constants included in Eqn 3).

Profile power is the power needed to overcome the drag of the wings during flight, parasitic power is the power needed to overcome body drag, and induced power is the power needed to support the weight of the bird during flight. For calculations of net rate of energy gain, \(P_f\) is converted to chemical power, the rate of fuel energy consumption, by assuming a conversion efficiency of 0.23. The body drag coefficient, one of the constants used to calculate \(P_{\text{par}}\), is set to 0.1 (Pennycuick et al., 1996). The power of soaring flight \(P_s\) is a constant multiple \((c)\) of the basal metabolic rate (BMR, in W) and is independent of speed (see Eqn 4):

\[
P_s = c \cdot \text{BMR}.
\]  
(4)

### Table 1. List of abbreviations and their respective descriptions and units

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
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<tbody>
<tr>
<td>BMR</td>
<td>Basal metabolic rate</td>
<td>W</td>
</tr>
<tr>
<td>(c)</td>
<td>Constant multiple of BMR for soaring flight</td>
<td>–</td>
</tr>
<tr>
<td>(D)</td>
<td>Travel distance</td>
<td>m</td>
</tr>
<tr>
<td>(E_n)</td>
<td>Foraging energy gain function</td>
<td>W</td>
</tr>
<tr>
<td>(P)</td>
<td>Power for flight</td>
<td>W</td>
</tr>
<tr>
<td>(P_f)</td>
<td>Power for flapping flight</td>
<td>W</td>
</tr>
<tr>
<td>(P_{\text{ind}})</td>
<td>Induced power</td>
<td>W</td>
</tr>
<tr>
<td>(P_{\text{par}})</td>
<td>Parasite power</td>
<td>W</td>
</tr>
<tr>
<td>(P_{\text{pro}})</td>
<td>Profile power</td>
<td>W</td>
</tr>
<tr>
<td>(P_s)</td>
<td>Power for gliding/soaring flight</td>
<td>W</td>
</tr>
<tr>
<td>(R)</td>
<td>Net rate of energy gain</td>
<td>W</td>
</tr>
<tr>
<td>(R_f)</td>
<td>R for flapping flight</td>
<td></td>
</tr>
<tr>
<td>(R_s)</td>
<td>R for soaring flight</td>
<td></td>
</tr>
<tr>
<td>(t_p)</td>
<td>Patch time (time for feeding)</td>
<td>s</td>
</tr>
<tr>
<td>(t)</td>
<td>Travel time between patches</td>
<td>s</td>
</tr>
<tr>
<td>(V_a)</td>
<td>Air speed</td>
<td>m s(^{-1})</td>
</tr>
<tr>
<td>(V_g)</td>
<td>Ground speed</td>
<td>m s(^{-1})</td>
</tr>
<tr>
<td>(V_{\text{mp}})</td>
<td>Minimum power air speed</td>
<td>m s(^{-1})</td>
</tr>
<tr>
<td>(V_{\text{me}})</td>
<td>Maximum range air speed</td>
<td>m s(^{-1})</td>
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</table>

### Table 2. Biometric parameters and aerodynamic flight performance predictions for black-headed gull and lesser black-backed gull

<table>
<thead>
<tr>
<th></th>
<th>Black-headed gull</th>
<th>Lesser black-backed gull</th>
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</thead>
<tbody>
<tr>
<td>Mass (kg)</td>
<td>0.285</td>
<td>0.77</td>
</tr>
<tr>
<td>Wing span (m)</td>
<td>0.967</td>
<td>1.43</td>
</tr>
<tr>
<td>Wing area (m(^2))</td>
<td>0.0992</td>
<td>0.243</td>
</tr>
<tr>
<td>Aspect ratio</td>
<td>9.43</td>
<td>8.52</td>
</tr>
<tr>
<td>BMR (W)</td>
<td>1.53</td>
<td>3.14</td>
</tr>
<tr>
<td>(\alpha) (Eqn 3)</td>
<td>1.1</td>
<td>1.1</td>
</tr>
<tr>
<td>(\beta) (Eqn 3)</td>
<td>19.06</td>
<td>5.7</td>
</tr>
<tr>
<td>(\gamma) (Eqn 3)</td>
<td>0.0004</td>
<td>0.0002</td>
</tr>
</tbody>
</table>

Values for mass, wing span and wing area for the lesser black-backed gull are taken from Bruderer and Boldt (Bruderer and Boldt, 2001). Other variables are derived (for calculations, see Appendix in supplementary material).
As suggested (Hedenström, 1993), \( c \) is conservatively set to 3. Values may be even lower, as found for certain sea birds (Weimerskirch et al., 2000; Weimerskirch et al., 2003). The cost of gliding flight of the herring gull, for example, was calculated as approximately 2.4 times the resting metabolic rate (Baudinette and Schmidt-Nielsen, 1974). Note that analogous to the subscripts for \( R \) and \( R_o \) and \( R_t \) refer to net rate of energy gain for foraging and soaring flight respectively. The biometric parameters required in Eqn 3 and 4 for the black-headed gull and lesser black-backed gull are specified in Table 2. All aerodynamic calculations and data analyses were performed in MATLAB 6.5.

Our expression of \( R \) is comparable to other studies where \( R \) is expressed as the difference between the gross rate of energy gain (the first term in Eqn 1) and the cost or energy expenditure (the second term in Eqn 1) (e.g. Hedenström and Alerstam, 1995; Bautista et al., 1998; Bautista et al., 2001). One of the central assumptions about the net rate of energy gain is the decreasing profit with higher rates of energy expenditure (Ydenberg and Hurd, 1998). In the next section we show how \( R \) can be calculated for different modes of flight, using measured values for ground and air speed.

**Combining measurements and models**

Eqn 1–4 are solved using measured combinations of ground speed and air speed, using the following parameter values to calculate net rate of energy gain: \( E_n = 20 \text{ W}, \ D = 10000 \text{ m}, \ t_p = 1800 \text{ s}. \) Similar values for travel distance, \( D \) (Horton et al., 1983; Gorke and Brandl, 1986; Prevot-Julliard and Lebreton, 1999; Baxter et al., 2003), foraging time \( t_p \) and flight duration \( t_i \) (Morris and Black, 1980; Gorke and Brandl, 1986) have been reported in field studies for different species of gulls. At a given combination of ground and air speed the model calculates the rate of net energy gain for both flapping and soaring flight. We focus on the relative difference between net energy gain for flapping and soaring flight to explain flight behavior rather than the absolute values for net energy gain. Reasons for this are the uncertainties in the energy gain function \( E_n \) and \( t_p \) as well as in the calculation of \( P \) (see also Discussion).

**Results**

**Predictions from optimal foraging and aerodynamic theory**

By applying Eqn 1–4 and the biometric characteristics (Table 2) of each gull species, to a range of air speed \( (V_g) \) and ground speed \( (V_a) \) from 5 to 25 m \text{s}^{-1}, we obtained patterns of net rate of energy gain \( (R) \) for flapping and soaring flight calculated for equal \( V_a \) and \( V_g \) (Fig. 2). The assumption of equal \( V_a \) and \( V_g \) is not required in our analysis but made here just to enable a two-dimensional graphical display of model sensitivities. If a bird flies at the same air and ground speed regardless of flight strategy, the net rate of energy gain is always higher for soaring flight than for flapping flight. Nevertheless there is a range of flight speeds where \( R \) is similar for both flight strategies; this range is wider for black-headed gulls than it is for lesser black-backed gulls. This is due to the much higher cost of flapping compared to soaring flight in lesser black-backed gulls. The difference in \( R \) between the two flight strategies increases with very low and very high air and ground speed combinations. However, the increase in \( R \) is much steeper for flapping flight at low speeds than at high speeds and may even result in energy loss. This implies that selecting flapping flight at the lower flight speeds is much more costly during foraging than at higher flight speeds.

The shape of \( R \), as a function of \( V_a \) and \( V_g \), changes with different combinations of \( E_n \) and \( D \) (Fig. 2). For example, if flight distance \( (D) \) decreases, the range of air and ground speeds where flapping and soaring flight result in similar net rate of energy gain increases (Fig. 2C,D). Furthermore, the net energy gain at lower air speeds increases. If however, the energy gain function \( (E_n) \) decreases, \( R \) decreases (Fig. 2E,F). The sensitivity of \( R \) to changes in \( t_p \) is not evaluated, because the parameter is confounded with \( E_n \) and \( D \).

The relationship between \( V_a \) and \( V_g \) and net energy gain is nonlinear. By plotting the net rate of energy gain or the difference in net energy gain between soaring and flapping flight \( (R_s-R_f) \) in relation to multiple combinations of \( V_a \) and \( V_g \), we can visually compare the result of different flight speed combinations (Fig. 3). If gulls maximize their net energy gain during foraging flights, then combinations of high \( V_a \) and low \( V_g \) as well as low \( V_g \) and high \( V_a \) are not expected, especially
Fig. 2. Net rate of energy gain (W) of black-headed gulls (A,C,E) and lesser black-backed gulls (B,D,F) for flapping (broken line) and soaring flight (solid line) solved for equal air speeds and ground speeds (m s\(^{-1}\)). (A,B) \(E_n=20\) W, \(D=10000\) m, (C,D) \(E_n=20\) W, \(D=5000\) m, (E,F) \(E_n=10\) W, \(D=10000\) m. \(t_p\) is kept constant because its effect on \(R\) is inverse to that on \(D\).

Fig. 3. The net energy gain (W) for flapping (\(R_{\text{flap}}; A,B\)) and soaring (\(R_{\text{soar}}; C,D\)) and the difference between \(R_{\text{soar}}\) and \(R_{\text{flap}}\) (E,F) considering different combinations of air speed (\(V_a\) m s\(^{-1}\)) and ground speed (\(V_g\) m s\(^{-1}\)) for black-headed gulls (A,C,E) and lesser black-backed gulls (B,D,F). Parameter estimates for calculating \(R\) are as follows: \(E_n=20\) W, \(D=10000\) m, \(t_p=1800\) s.
during flapping flight. The power needed for flight varies with $V_a$ in flapping flight, but is constant in soaring flight. Therefore, increased ground speeds results in higher net energy gain regardless of air speeds during soaring. The difference in $R$ between flight strategies is highest for combinations of high $V_a$ and low $V_g$ and low $V_a$ and $V_g$ and is much higher in lesser black-backed gulls than in black-headed gulls.

**Measuring flight speed, direction and altitude**

The mean measured $V_a$, $V_g$ and flight altitude of both gull species are summarized in Table 3. The mean air speeds of black-headed gulls and lesser black-backed gulls, regardless of flight strategy, were higher than the predicted minimum power speed $V_{mp}$ (9.57 m s$^{-1}$ and 10.96 m s$^{-1}$, respectively) and lower than the predicted maximum range speed $V_{mr}$ (15.7 and 17.8 m s$^{-1}$, respectively). $V_{mp}$ and $V_{mr}$ were calculated on the basis of the data in Table 2 (see Appendix in supplementary material). For both species, $V_6$ of both flight strategies combined was positively and significantly related to $V_a$ (black-headed gull: $V_6=1.66 \cdot V_a+0.93$, $r^2=0.74$, $P<0.001$, Fig. 4A; lesser black-backed gull: $V_6=1.61 \cdot V_a+0.95$, $r^2=0.65$, $P<0.001$, Fig. 4B). Flight directions (air and ground) for both species and both flight strategies did not differ significantly from a uniform distribution (Raleigh Test of uniformity). In this study, the maximum flight altitude of both gull species did not exceed 1000 m (Table 3) (for more details, see Shamoun-Baranes et al., 2006).

**Flight strategy**

The ratio of the number of soaring and gliding to flapping flight tracks was 2.56 in lesser-black-backed gulls compared to 0.75 in black-headed gulls. The frequency of soaring flight was higher than flapping flight at lower air speeds for both species (Fig. 4). For both species and flight strategies, the observations were normally distributed over ground and air speeds, on the basis of a Lilliefors test (Lilliefors, 1967). The soaring to flapping ratio increased at higher winds speeds in both species. For wind speeds $\leq 5$ m s$^{-1}$, the soar/flap ratio was 0.52 for black-headed gulls and 2 for lesser black-backed gulls. For winds speeds $>5$ m s$^{-1}$, the ratio was 7 for black-headed gulls and 3.88 for lesser black-backed gulls. There were no tracks of black-headed gulls at wind speeds above 7.0 m s$^{-1}$ where lesser black-backed gulls were recorded in soaring flight at a maximum wind speed of 11 m s$^{-1}$.

Table 3. Air speeds, ground speeds and flight altitudes for flapping and soaring/gliding flight of black-headed gulls and lesser black-backed gulls

<table>
<thead>
<tr>
<th></th>
<th>Black-headed gull</th>
<th>Lesser black-backed gull</th>
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</thead>
<tbody>
<tr>
<td>$V_a$ (m s$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flapping</td>
<td>14.13±3.18</td>
<td>14.54±2.63</td>
</tr>
<tr>
<td>Soaring</td>
<td>13.64±4.42</td>
<td>13.90±4.37</td>
</tr>
<tr>
<td>$V_g$ (m s$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flapping</td>
<td>14.67±3.94</td>
<td>13.64±3.49</td>
</tr>
<tr>
<td>Soaring</td>
<td>14.13±4.27</td>
<td>15.50±4.96</td>
</tr>
<tr>
<td>Flight altitude (m)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flapping</td>
<td>132.0±71.3</td>
<td>174.8±138.5</td>
</tr>
<tr>
<td>Soaring</td>
<td>225.8±139.4</td>
<td>298.3±152.85</td>
</tr>
<tr>
<td>Maximum</td>
<td>574.6</td>
<td>737.7</td>
</tr>
<tr>
<td>N</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flapping</td>
<td>28</td>
<td>27</td>
</tr>
<tr>
<td>Soaring</td>
<td>21</td>
<td>69</td>
</tr>
</tbody>
</table>

$V_a$, air speed; $V_g$, ground speed. Values are means and s.d. ($N$=number of observations).

Fig. 4. Observed ground speeds ($V_g$, m s$^{-1}$) and observed air speeds ($V_a$, m s$^{-1}$) during flapping (+) and soaring (○) flight for the black-headed gull (A) and the lesser black-backed gull (B). Regression lines are shown for each species and each flight strategy (solid line for soaring, broken line for flapping; the 1:1 line is included for reference purposes). The frequency distributions of $V_a$ and $V_g$ during soaring and flapping flight are presented along the respective axes at the right and top. The lines of the frequency distributions are shifted slightly along the category axis for display purposes.
Confounded (see Fig. 4), flapping ($R_s - R_f$) was greater than 6 W, for black-headed gulls (A) and lesser black-backed gulls (B). Parameter estimates for $R$ are as follows: $E_0=20$ W, $D=10000$ m, $t_p=1800$ s. As observed $V_a$ and $V_g$ values are highly confounded (see Fig. 4), $R$ was not plotted against both $V_a$ and $V_g$.

**Combining measurements and models**

Eqn. 1–4 were solved using measured $V_a$ and $V_g$ and observed flight strategy. The predicted values for $R$ solved for the observed combination of flight strategy, $V_a$ and $V_g$, were always positive and within the same range of values for both species (Fig. 5). The predicted difference in net energy gain between soaring and flapping ($R_s - R_f$) was also calculated with measured $V_a$ and $V_g$ combinations. For black-headed gulls, only small differences in $R$ ($\leq 3$ W) were predicted between flight strategies for the observed combinations of air speeds and ground speeds (Fig. 6). These values were slightly higher for lesser black-backed gulls. In all cases where the predicted $R_s - R_f$ was greater than 6 W, lesser black-backed gulls were observed soaring.

For descriptive purposes, the distribution of measured $V_a$ for each flight strategy is summarized with the normal probability distribution function (Fig. 7). This simplification of the data helps to clarify patterns in the data and can be used to predict the ratio between soaring and flapping flight, while providing an excellent fit with the measurements. For example, from the observations, we find that flapping flight is more predominant than soaring flight for $V_a$ between 10.8 and 18.5 m s$^{-1}$ for black-headed gulls and $V_a$ between 11.6 and 18.3 m s$^{-1}$ for lesser black-backed gulls. We can also derive a range of values where the soar/ flap ratio is <1 by applying other selection criteria, for example, based on calculated $R$ for each flight strategy and the difference in $R$ between flight strategies ($R_s - R_f$). The predicted ratios of soaring to flapping in relation to $V_a$ (calculated using the normal probability distributions shown in Fig. 7) are not significantly different from the observed ratio of soaring/flapping flight based on the $V_a$ range mentioned above (based on a Chi-square test, $\chi^2=0.06, P=0.99$, d.f.=3). The observed and predicted ratios of soaring to flapping are given in Table 4.
In our study, it is clear that wind speed and direction can strongly influence both the time and energy budget of a bird and hence the net rate of energy gain. If a bird attempts to maximize the net rate of energy gain then both the travel time (inversely related to ground speed) and cost of flight (a function of air speed) should be minimized. How a bird responds to wind can influence its ground speed (and hence travel time) as well as its air speed (influencing the cost of flight) and also, therefore, its flight strategy selection. As found in this study and several others (Pennycuick, 1982; Flint and Nagy, 1984; Rosen and Hedenström, 2001), the proportion of soaring flight increases with increasing wind speeds. Given the spatial and temporal resolution of our data and our model framework, however, like others, we cannot explain this relationship. Gulls over the sea used three predominant forms of flight: (1) flapping, (2) convective soaring (circling in thermal updrafts) and (3) linear soaring (soaring into the wind and increasing flight altitude) (Woodcock, 1940a; Woodcock, 1940b; Woodcock, 1975). These flight strategies were clearly associated with certain sea–air temperature and wind speed conditions. Perhaps the increasing proportion of soaring flight with increased wind speed is related to the flexibility of gulls to exploit a wide range of wind speeds by using different soaring techniques, as observed by Woodcock (Woodcock, 1940a; Woodcock, 1940b; Woodcock, 1975).

The relationship between flight strategy, energetics during foraging and weather will be influenced by the spatial foraging behavior of gulls. When gulls randomly search for food, soaring and flapping flight will occur in similar ratios for different wind directions. Alternatively, wind speeds and directions will have a strong influence on time and energy and hence flight strategy when there is a preference for a food source at a specific spatial location. A difference in flapping to soaring ratios for different flight directions would suggest the existence of a preferred feeding location. Several studies have shown that gull species such as black-headed gulls, lesser black-backed gulls and herring gulls show foraging site fidelity or predictable foraging movements (Morris and Black, 1980; Horton et al., 1983; Gorke and Brandl, 1986; Prevot-Julliard and Lebreton, 1999). If birds do not have a preferential direction when foraging than we may expect them to select flight directions in relation to wind. Soaring albatrosses (Order Procellariiformes) preferred foraging flight directions according to wind directions and achieved higher ground speeds in tail and side winds, reducing the cost of soaring flight (Weimerskirch et al., 2000).

The cost of flight is an additional factor influencing our parameter space. If, for example, the energetic cost of flapping flight is lower than presently calculated, the range of overlap where both flight strategies will have a similar energetic benefit will increase. The predictions in this study assume constant flapping vs constant soaring. However, gulls often use a mixture of flap-gliding and appear to be quite flexible in their flight strategy selection. The heart rate of herring gulls during flapping flight was highly variable (Kanwisher et al., 1978) and may be due to this flexibility in flap-gliding strategy. By

### Table 4. Observed and predicted soar/flap ratio for black-headed gulls and lesser black-backed gulls

<table>
<thead>
<tr>
<th>Soar/Flap ratio</th>
<th>Black-headed gull</th>
<th>Lesser black-backed gull</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;1</td>
<td>1.63</td>
<td>1.79</td>
</tr>
<tr>
<td>&lt;1</td>
<td>0.83</td>
<td>0.72</td>
</tr>
<tr>
<td>Predicted</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;1</td>
<td>1.69</td>
<td>2.13</td>
</tr>
<tr>
<td>&lt;1</td>
<td>0.78</td>
<td>0.69</td>
</tr>
</tbody>
</table>

The criteria for calculating soar/flap ratio <1 for black-headed gulls are \(10.8 \geq V_a \leq 18.5\) m s\(^{-1}\) and \(11.6 \geq V_a \leq 18.3\) m s\(^{-1}\) for lesser black-backed gulls. The soar/flap ratio <1 was predicted by calculating the ratio of surface of soaring to the surface of flapping within the corresponding gray areas (see Fig. 7) for each species. The observed values do not differ significantly from the predicted ones according to a Chi-square test (\(\chi^2=0.06, P=0.99\)).

### Discussion

This study outlines a model that brings together foraging, flight energetics and flight behavior theories. The observations made during this study strongly support the hypothesis that flight and foraging energetics influence the selection of flight strategy during travel between foraging sites. When testing different combinations of air speed and ground speed and different parameter sets, we arrive at a theoretical range of flight speeds where soaring is much more beneficial than flapping. Furthermore, with our model framework we reach a high degree of explanation of the observed ratio of soaring to flapping flight. In accordance with theoretical predictions, when the predicted net rate of energy gain for soaring is much larger than for flapping, a bird selects soaring flight. This is also reflected in the higher proportion of soaring flight for lesser black-backed gulls than black-headed gulls. Combinations of ground and air speed that would result in very low or negative net rate of energy gain were not found within the tested parameter space. Although energetics is a proximate mechanism influencing the selection of flight strategy other factors may also be influential.

One main factor that may influence flight strategy is the weather. Meteorological conditions may not only influence the ability of a bird to flap or soar but also the energy expenditure or time needed for flight. Although the relationship between meteorological conditions and gull flight strategy is the focus of a different study (E. van Loon and J. Shamoun-Baranes, manuscript in preparation), we briefly discuss the potential influence of meteorological conditions on flight strategy selection. The soaring flight behavior of raptors, storks and pelicans is strongly influenced by characteristics of the convective boundary layer (Kerlinger, 1989; Shannon et al., 2002; Shamoun-Baranes et al., 2003). Several studies have found a relationship between the flight strategy selection of different avian species and meteorological conditions (Woodcock, 1940a; Woodcock, 1940b; Woodcock, 1975; Bruderer et al., 1994; Spaar et al., 1998; Sergio, 2003).
Energetics and flight strategy selection

Efficiently using different flight strategies, gulls may take advantage of a wide range of air movements and quasi two-dimensional structures in the atmospheric boundary layer (Young et al., 2002). The cost of flight is determined in this study by Eqs 3 and 4. The accuracy and precision of these equations depend on model inputs as well as parameter uncertainty. Sometimes, these two sources of uncertainty interact in a complex way. For example, air density will influence the cost of flight at a given air speed. In our calculations, air density is set to 1.225 kg m⁻³. This is the air density according to the properties of the Standard Atmosphere at sea level with a barometric pressure of 1013.25 mb and a temperature 15°C in dry air (US Standard Atmosphere, 1976). However, air density is influenced by barometric pressure, temperature, and the amount of water vapor in the air (Holton, 2004). Considering Standard Atmosphere properties, density decreases with altitude (at 1000 m, air density=1.11 kg m⁻³) resulting in decreasing parasite power and increasing induced power. In this case, observations of barometric pressure with altitude as well as parameter estimates in the parasite power and induced power equations are interacting. An example of parameter uncertainty is the conversion of mechanical power to metabolic power output during flight. In this study, we apply a constant conversion efficiency of 0.23 for both species; however, a flight muscle efficiency of 0.18 was found to be more accurate for birds the size of a starling (Sturnus vulgaris) weighing approximately 100 g (Ward et al., 2001). Alternatively, the conversion efficiency may scale with mass (Bishop, 2005). Other factors such as the body drag coefficient (Hedenström and Liechti, 2001; Maybury and Rayner, 2001) or the shape of the power curve itself (Dial et al., 1997; Rayner, 2001; Tobalske et al., 2003) are still being debated in the literature. In order to appropriately determine the sensitivity of our model to different inputs and parameter settings in Eqs 2, 3, and 4, a full sensitivity analysis, as was conducted by Spedding and Pennycook for the flight power curve (Spedding and Pennycook, 2001), is needed. This is beyond the scope of this paper but will be a topic of future research.

On the basis of our study, we may articulate some new, testable hypotheses about flight strategy during foraging. Gulls may show a higher tendency for flapping flight (1) when soaring is not possible or less efficient than flapping (for example due to meteorological conditions); (2) when flapping is possible at the range of flight speeds where the difference between soaring and flapping net energy gain is minimal and the net energy gain is above a certain critical value. As a function of patch quality, average flight distance to patches and average feeding duration, gulls will change the ratio of soaring to flapping flight. With increasing foraging distances, the range of flight speeds where net energy gain is similar between flight strategies decreases. Black-headed gulls (Gorke and Brandl, 1986; Prevot-Julliard and Lebreton, 1999) and herring gulls (Belant et al., 1993) showed increasing foraging distances later in the breeding season. It can therefore be expected that gulls will show a higher proportion of soaring flight later in the breeding season as foraging distances increase and the difference in net energy gain during soaring and flapping increases.

The fit between our model and the observations is very close. Considering the spatial and temporal scale of our measurements, and the lack of exact information on gull activity, we think that more extensive models would not increase our insight. We expect that a high resolution, homogeneous dataset for both weather and flight speeds over longer periods of time, accompanied by time-budget information for the birds, would not only improve the fit between our current model and measurements but also, and more importantly, further our understanding of the factors influencing flight strategy selection.

We especially thank Hans van Gasteren and Jelmer van Belle, Royal Netherlands Air Force, for their fieldwork in collecting and processing the gull tracking data. We also thank Willem Bouten and two anonymous reviewers for their constructive comments on a previous version of this manuscript. Meteorological data were provided by the Royal Netherlands Meteorological Institute (KNMI) and we thank H. Klein Baltink for his feedback. This study was conducted within the Virtual Laboratory for e-Science project (www.vl-e.nl), supported by a BSIK grant from the Dutch ministry of education, culture and science and the ICT innovation program of the ministry of economic affairs.

References
Hedenström, A. (1993). Migration by soaring or flapping flight in birds – the


Online Appendix

Matlab code to calculate power cost of flight for black-headed gull and lesser black-backed gull on the basis of one or more air speed values ($V_a$, m s$^{-1}$) and several physical parameters (all-up mass in kg, wing span in m, wing area in m$^2$, aspect ratio, and basal metabolic rate in W).

```matlab
% pennypower.m
% %
% % A function to calculate power required by a bird at a given airspeed
% % when using flapping and soaring flight, using the equations suggested
% % by Pennycuick.
% %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% June 20, 2006
% This function was used in the following study:
% % Shamoun-Baranes, J. and van Loon, E. (in press) Energetic influence on gull
% flight strategy selection.
% % Journal of Experimental Biology.
% % Please cite the above reference when using this script.
% % If you have any questions don't hesitate to contact
% % Judy Shamoun-Baranes (shamoun@science.uva.nl) or
% % Emiel van Loon (vanloon@science.uva.nl)
% %
% %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% [cl,Pfl,Pgl] = pennypower(V,m,ws,wa,bmr,[Vmp],[plt_opt])
% % cl = index, indicating whether a bird is expected to flap (1) or soar (2)
% % Pfl = power needed for flapping flight (in Watt)
% % Pgl = power needed for gliding flight  (in Watt)
% % V = the airspeed for which Pfl and Pgl have to be calculated (m/s)
% % m = all-up mass, this is the sum of the body mass with the
% %   crop empty (empty mass), plus the mass of any food that
% %   the bird may be carrying in its crop (kg).
% % ws = wing span (m)
% % wa = wing area (m$^2$)
% % bmr = basal metabolic rate (W )
% % Vmp = minimum power velocity, determined visually with (vmp_calc)
% %    if it is not given or empty it is determined automatically (m/s)
% % plt_opt = whether a plot is desired (1) or not (0), default is 1
% %
% % The source for this script is Pennycuick's flight program version 1.14
% (January 2004).
% url: http://www.bio.bris.ac.uk/people/staff.cfm?key=95
```
153 pp.

% An example of how to use this function:
% e.g. using the physical parameters for a black-headed gull (bhg)
% and lesser black backed gull (lbbg), with automatic calculation of Vmp:
% [cl_bhg,Pfl_bhg,Pgl_bhg] = pennypower(5:0.5:20,0.285,0.967,0.0992,1.53);
% text(0.6,0.85,'Black headed gull','fontsize',14);
% [cl_lbbg,Pfl_lbbg,Pgl_lbbg] = pennypower(5:0.5:20,0.77,1.43,0.243,3.14);
% text(0.6,0.85,'Lesser black backed gull','fontsize',14);
%
% and with values for Vmp, provided a-priori:
% [cl_bhg,Pfl_bhg,Pgl_bhg] = pennypower(5:0.5:20,0.285,0.967,0.0992,1.53,10);
% text(0.6,0.85,'Black headed gull','fontsize',14);
% [cl_lbbg,Pfl_lbbg,Pgl_lbbg] = pennypower(5:0.5:20,0.77,1.43,0.243,3.14,11);
% text(0.6,0.85,'Lesser black backed gull','fontsize',14);

% Emiel van Loon & Judy Shamoun-Baranes, 2005
function [cl,Pfl,Pgl]=pennypower(V,m,ws,wa,bmr,Vmp,plt_opt)

%%%%%%%%%%%%%%%%%%
% Input handling %
%%%%%%%%%%%%%%%%%%
if ~exist('bmr','var')
    help pennypower
    return
end

% Aspect ratio
% the ratio of the wing span to the mean chord. The most convenient way to
calculate it is:
    ar = ws^2/wa;

if ~exist('plt_opt','var')|isempty(plt_opt),
    plt_opt = 1;
end
if ~exist('Vmp','var')|isempty(Vmp),
    Vmp = vmp_calc(m,ws,ar);
end

%%%%%%%%%%%%%%%%%%
% Constants %
%%%%%%%%%%%%%%%%%%
rho = 1.23; % air density under standard conditions in kg/m^3
g = 9.81; % acceleration due to gravity in m/s^2
ppc = 8.4; % profile power constant
k = 1.2; % induced power factor
h = 0.23; % conversion efficiency
R = 1.1; % respiration factor
bdc = 0.1; % body drag coefficient

%%%%%%%%%%%%%%%%%%% % Derived constants % %%%%%%%%%%%%%%%%%%%%

% The body frontal area (Sb) is estimated from the all-up mass, % using an empirical formula (in m^2)
Sb = 0.00813 * m^0.666;

% The equivalent flat-plate area (A) is the body frontal area % times the body drag coefficient (in m^2)
A = Sb * bdc;

% The disc area (Sd) is the area of a circle, whose diameter % is equal to the wing span (in m^2)
Sd = pi * ws^2 / 4;

%%%%%%%%%%%%%%%%%%% % Main calculations % %%%%%%%%%%%%%%%%%%%%

% Calculate Pind and Ppar at Vmp, % subsequently Pam as the sum of these % and finally Ppro
Ppar = rho * A * V.^3 ./ 2;
Pind = k * m^2 * g^2 ./ ( 2 * rho * Sd * V );

% Converting the mechanical power to chemical power
Pf1 = R * ( Pfl_mech + h*bmr ) / h;
% Power consumption in soaring flight (ref. Hedenstrom 1993 pg 356 bottom)
Pgl = 3 * bmr;
% calculate the parameters for the simplified equation:
% Pf = a + b/V + c*V^3

a = R;
b = R * k * m^2 * g^2 / (2 * rho * Sd);
c = rho * A / 2;

disp('The simplified equation for Pf is: Pf = a + b/V + c*V^3 ')
disp('For the current inputs, the parameters in this equation are:')
disp(['a = ' num2str(a)]);
disp(['b = ' num2str(b)]);
disp(['c = ' num2str(c)]);

% Make graphs
%
if plt_opt==1
    figure
    ph = plot(V,Pfl,'k-',[min(V) max(V)],[Pgl Pgl],'k:'); ah=gca;
    set(ah,'fontsize',14); box off;
    set(ph(:),'linewidth',1.5);
    xlabel('V_a (m/s)');
    ylabel('P (Watt)');
    lh=legend('flapping','soaring/gliding',2); set(lh,'fontsize',14);
    legpos = get(lh,'Position');
    axes('position',[0 0 1 1]); axis([0 1 0 1]); hold on; axis off;
    text(0.1+legpos(1) ,0.95*legpos(2),['Vmp = ' num2str(Vmp)],'fontsize',14);
end

cl = (Pgl>Pfl) + 1;

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% helper-function to calculate Vmp on the basis of m, ws and ar %
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

function [Vmp] = vmp_calc(m,ws,ar)
% [Vmp]=vmp_calc(m,ws,ar)
%
% with m = mass (kg)
%  ws = wing span (m)
%  ar = aspect ratio (m^2/m^2)
%
% example for black headed gull:
%  [Vmp_bhg] = vmp_calc(0.285,0.967,9.43)
%
% example for lesser black backed gull:
%  [Vmp_lbbg] = vmp_calc(0.77,1.43,8.52)
%

%%%%%%%%%%%%%
% Constants %
vstep = 0.1; \quad \% \text{for plotting}
rho = 1.23; \quad \% \text{air density in kg/m}^3
g = 9.81; \quad \% \text{acceleration due to gravity in m/s}^2
ppc = 8.4; \quad \% \text{profile power constant}
k = 1.2; \quad \% \text{induced power factor}
bdc = 0.1; \quad \% \text{body drag coefficient}

\% \text{Derived constants} \\
\% \text{The body frontal area (Sb) is estimated from the all-up mass,}
\% \text{using this empirical formula: [in m}^2]\n
Sb = 0.00813 * m^{(2/3)};

\% \text{The equivalent flat-plate area (A) is the body frontal area}
\% \text{times the body drag coefficient [in m}^2]\n
A = Sb * bdc;

\% \text{The disc area (Sd) is the area of a circle, whose diameter}
\% \text{is equal to the wing span: [Sd in m}^2]\n
Sd = \pi * ws^2 / 4;

V = 1:vstep:20;

Pind = k * m^2 * g^2 ./ ( 2 * rho * Sd * V );
Ppar = rho * A * V.^3 ./ 2;
Pmech = Ppar + Pind;

Pind_der = -k * m^2 * g^2 ./ ( 2 * rho * Sd * V.^2 );
Ppar_der = 3 * rho * A * V.^2 / 2;
Pmech_der = Pind_der + Ppar_der;

[Pmech_min,idx] = min(abs(Pmech_der-0));
Vmp = V(idx);