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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.

Supplementary material available online at
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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

(*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 (Hollandse 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:

$$R = \frac{1}{t_p + t_t}\left(\int_0^{t_p} E_n(t)\mathrm{d}t - \int_0^{t_t} P(t)\mathrm{d}t\right), \qquad (1)$$

where R is net rate of energy gain (W), $E_n(t)$ 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_t 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 $E_n(t)$ 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_t and $P(t)$ in Eqn 1 affect net energy

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

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

gain of a species (t_p and E_n 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

$$\int_0^{t_p} E_n(t)\mathrm{d}t \, .$$

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

$$\int_0^{t_p} E_n(t)\mathrm{d}t$$

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

$$\int_0^{t_t} P(t)\mathrm{d}t$$

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

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

	Black-headed gull	Lesser black-backed gull
Mass (kg)	0.285	0.77
Wing span (m)	0.967	1.43
Wing area (m^2)	0.0992	0.243
Aspect ratio	9.43	8.52
BMR (W)	1.53	3.14
α (Eqn 3)	1.1	1.1
β (Eqn 3)	19.06	5.7
γ (Eqn 3)	0.0004	0.0002

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).

Combining this with a fixed distance between food patches, travel time (t_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:

$$R = \frac{E_n t_p}{t_p + t_t} - \frac{P t_t}{t_p + t_t} \, . \qquad (2)$$

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_{pro}), parasite power (P_{par}) and induced power (P_{ind}), Eqn 3:

$$P_f = P_{pro} + P_{par} + P_{ind} = \alpha + \frac{\beta}{V_a} + \gamma \cdot V_a^3 \, , \qquad (3)$$

(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_{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):

$$P_s = c \cdot BMR \, . \qquad (4)$$

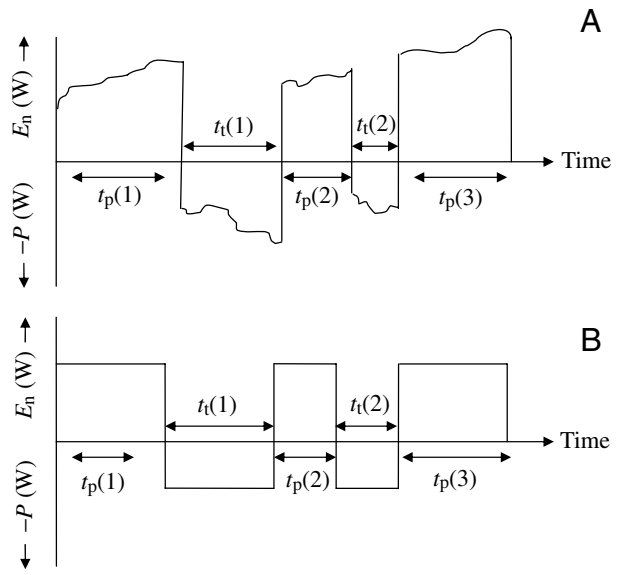

Fig. 1. Schematic representation of Eqn 1 and 2, showing our conceptualization of a bird's energy balance. Birds gain energy during foraging and lose energy when traveling between food patches. The switch between these modes is instantaneous. (A) The general case where energy gain, $E_n(t_p)$, and the power required for flight, $P(t_t)$, are functions of time (Eqn 1). (B) The simplification used in this study where E_n and P are constant over time (Eqn 2). The total travel time is in both cases calculated by the sum $t_t=\Sigma_i t_t(i)$ and the time spent foraging is calculated by $t_p=\Sigma_i t_p(i)$. Note that P is given in positive values in Eqn 1 and 2, so that $-P$ is used on the negative part of the vertical axis.

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 P, R_f and R_s refer to net rate of energy gain for flapping 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 W, D=10000 m, t_p=1800 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_t (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_a) and ground speed (V_g) from 5 to 25 m 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 decrease 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

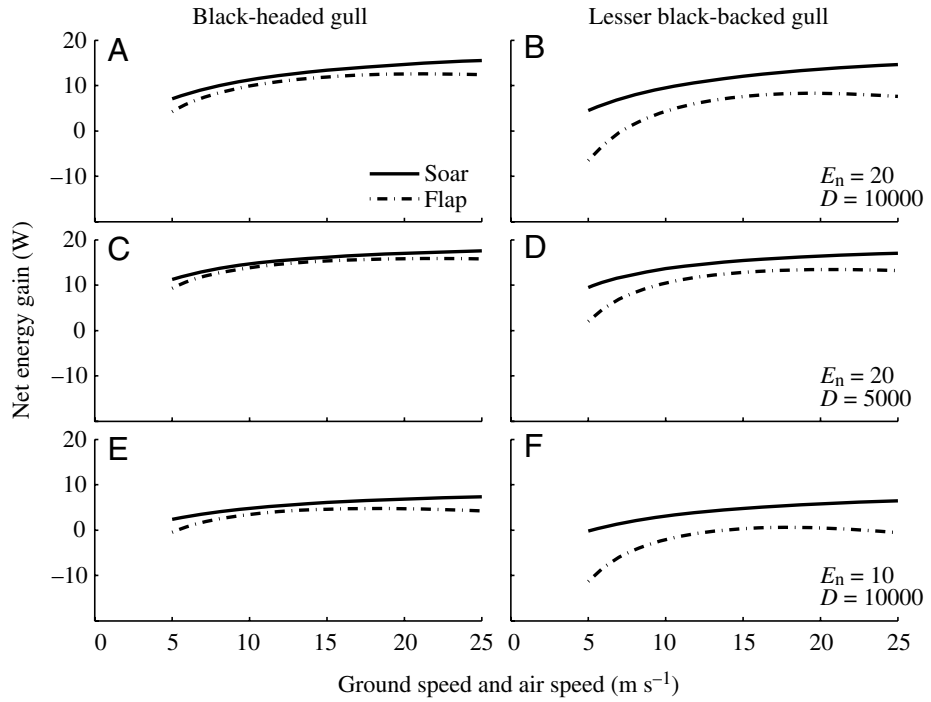

Fig. 2. Net rate of energy gain (W) of black-headed gulls (A,C,E) and lesser black-backed gulls (B,D,F) for flapping (broken line) and soaring flight (solid line) solved for equal air speeds and ground speeds (m s^{-1}). (A,B) E_n=20 W, D=10000 m, (C,D) E_n=20 W, D=5000 m, (E,F) E_n=10 W, D=10000 m. t_p is kept constant because its effect on R is inverse to that on D.

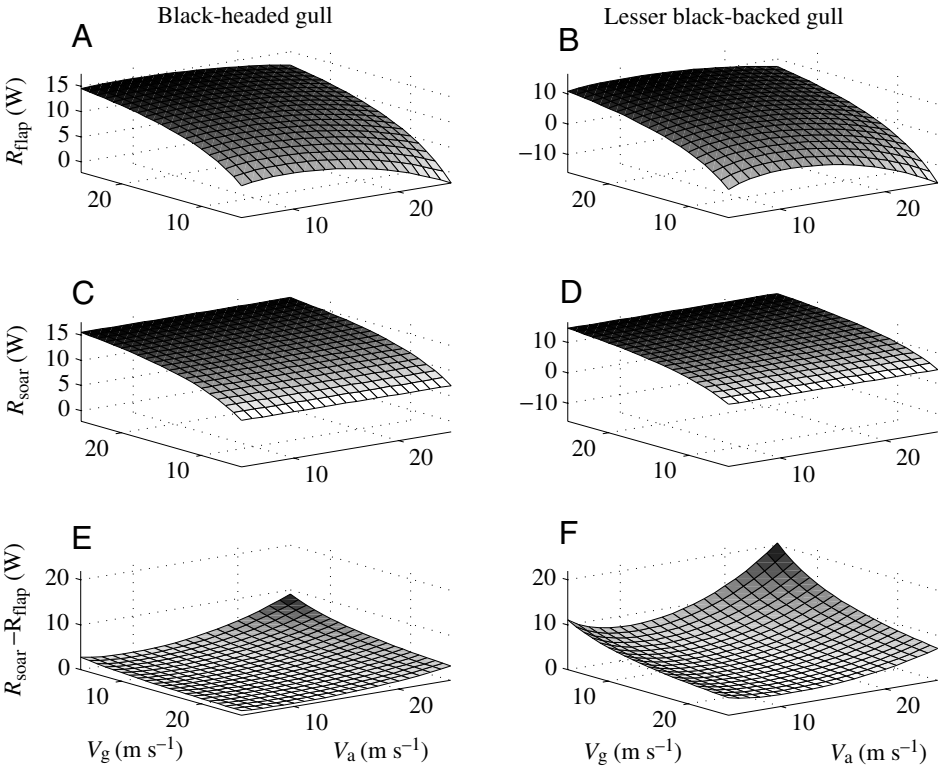

Fig. 3. The net energy gain (W) for flapping (R_{flap}; A,B) and soaring (R_{soar}; C,D) and the difference between R_{soar} and R_{flap} (E,F) considering different combinations of air speed (V_a m s^{-1}) and ground speed (V_g m s^{-1}) for black-headed gulls (A,C,E) and lesser black-backed gulls (B,D,F). 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.

Measured 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 then 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_g of both flight strategies combined was positively and significantly related to V_a (black-headed gull: V_g=1.66·V_a+0.93, r^2=0.74, P<0.001, Fig. 4A; lesser black-backed gull: V_g=1.61·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-blacked 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 ≤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} whereas 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*

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

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

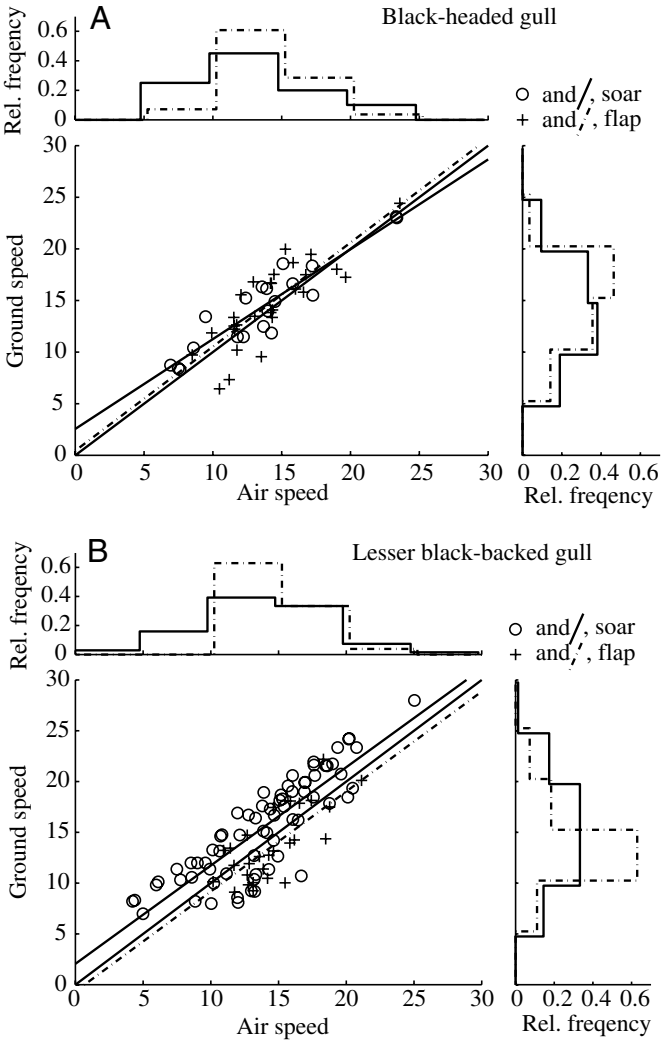

Fig. 4. Observed ground speeds (V_g, m s^{-1}) and observed air speeds (V_a, m s^{-1}) during flapping (+) and soaring (○) flight for the black-headed gull (A) and the lesser black-backed gull (B). Regression lines are shown for each species and each flight strategy (solid line for soaring, broken line 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.

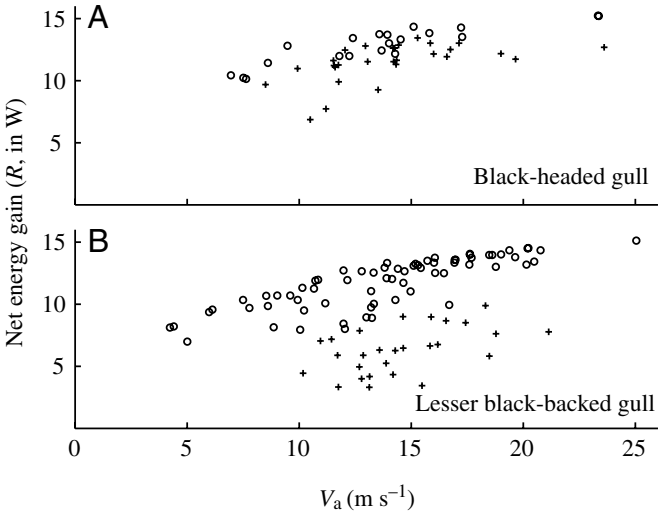

Fig. 5. The predicted net energy gain (R, in W) calculated with observed ground speed (V_g), air speed (V_a) and flight strategy combinations. Different symbols (+ flapping, ○ soaring) represent the predicted R for a measured combination of V_g, V_a and flight strategy for black-headed gulls (A) and lesser black-backed gulls (B). Parameter estimates for R calculations are as follows: E_n=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.

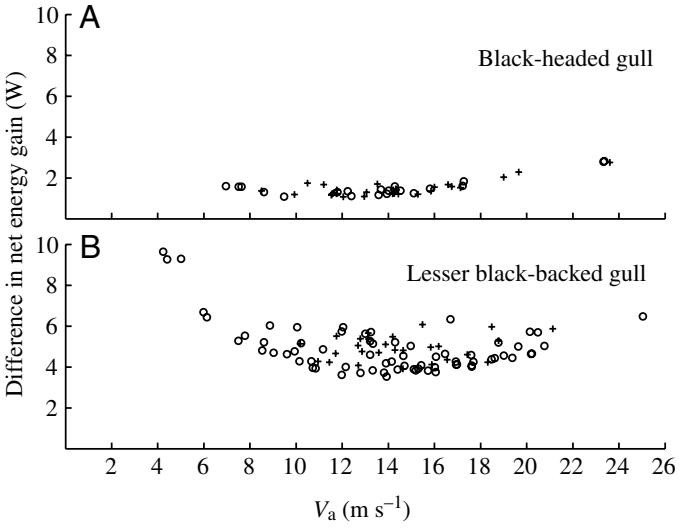

Fig. 6. The predicted differences in net energy gain between soaring (○) and flapping (+) flight (R_s–R_f) calculated with observed combinations of air speed (V_a, m s^{-1}), ground speed (V_g, m s^{-1}) and flight strategy, for black-headed gulls (A) and lesser black-backed gulls (B). Parameter estimates for R are as follows: E_n=20 W, D=10000 m, t_p=1800 s. As observed V_a and V_g values are highly confounded (as shown in Fig. 4), R_s–R_f 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 (⩽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

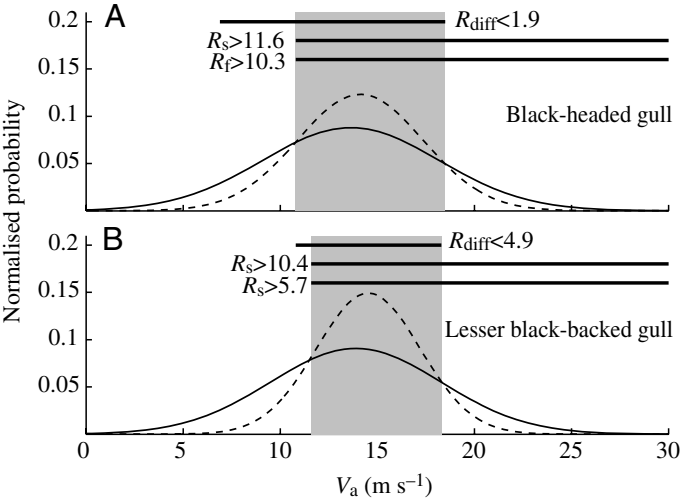

Fig. 7. The estimated normal probability distribution of air speeds (V_a, m s^{-1}) during flapping (broken line) and soaring flight (solid line) for the black-headed gulls (A) and lesser black-backed gulls (B). This simplification of the data can be used to predict, for example, the range of V_a where the soar/flap ratio is <1 (area shaded in gray). Thick solid lines at the top of each figure represent alternative selection criteria that can be used to determine the soar/flap ratio <1 (area shaded in gray): for example, where R_{diff}<1.9 W and R_s>11.6 (black-headed gull).

mentioned above (based on a Chi-square test, χ^2=0.06, P=0.99, d.f.=3). The observed and predicted ratios of soaring to flapping are given in Table 4.

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

Soar/Flap ratio	Black-headed gull	Lesser black-backed gull
Observed		
>1	1.63	1.79
<1	0.83	0.72
Predicted		
>1	1.69	2.13
<1	0.78	0.69

The criteria for calculating soar/flap ratio <1 for black-headed gulls are $10.8 \geqslant V_a \leqslant 18.5$ m s^{-1} and $11.6 \geqslant V_a \leqslant 18.3$ 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 (χ^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).

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 Procellariformes) 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

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 Eqn 3 and 4. The accuracy and precision of these equations depends on model input 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 Eqn 2, 3 and 4 a full sensitivity analysis, as was conducted by Spedding and Pennycuick for the flight power curve (Spedding and Pennycuick, 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 period. 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.

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