Flight speeds of parent birds feeding nestlings: maximization of foraging efficiency or food delivery rate?

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We examined the flight behaviour of female Lapland longspurs (Calcarius lapponicus) foraging during the nestling period to determine whether they flew at speeds maximizing the overall rate of energy delivery to their nestlings (Vry), or at speeds maximizing the distance travelled per unit energy expended (Vmr), as predicted by different models. The average flight speed of females was slower when they flew to closer feeding sites, suggesting that acceleration was an important component of these flights. We therefore included the cost of acceleration into the flight-speed models. Longspurs flew slightly faster, on average, than our predicted speeds for maximizing the distance travelled per unit energy expended (Vmr) but substantially lower than our predicted speeds for maximizing the overall rate of energy delivery to nestlings (Vry). The fact that longspurs did not fly faster at times of increased food availability is also consistent with maximizing the distance travelled per unit energy expended, but not with maximizing the overall rate of energy delivery. Based on other studies of parent birds feeding young, we expected that longspurs would adjust their flight speeds to maximize the overall rate of energy delivery to their young. Instead, their flight behaviour was more consistent with maximizing foraging efficiency (the ratio of energy collected to energy spent).

Introduction

For parent birds feeding altricial nestlings, the flight speed used when flying to and from foraging sites can be an important decision. As in other studies of foraging behaviour, we use the word “decision” when the birds perform one behaviour when they could have performed another (see also Stephens and Krebs 1986) and not to suggest that they made a conscious decision. Flight entails a high energy cost per unit time in relation to other activities (e.g., Utter and LeFebvre 1970; Tucker 1972), and while it may constitute a small proportion of a bird’s time budget, flight costs often represent a substantially larger proportion of total daily energy expenditures (e.g., Schartz and Zimmerman 1971; Walsberg 1977; Westerterp and Drent 1985). In addition, some parent birds make up to 500 foraging trips per day to gather food for their nestlings (Norberg 1981). Since both the rate of energy expenditure and the time spent in flight depend upon flight speed (Tucker 1972), the flight speed used could influence a parent bird’s ability to provide adequate nourishment for its young (Norberg 1981).

Flight speeds can also be useful to study when investigating whether a particular currency is maximized by parent birds (e.g., Welham and Ydenberg 1988). Many optimal foraging models assume that a forager maximizing its long-term net rate of energy gain (energy per unit time) will maximize its fitness (Stephens and Krebs 1986; Houston et al. 1988). However, recent studies have concluded that the behaviour of some foraging animals is consistent with maximizing foraging efficiency (the ratio of energy gained to energy spent) rather than a gain rate (e.g., Schmid-Hempel et al. 1985; Kacelnik et al. 1986; Schmid-Hempel 1987; Welham and Ydenberg 1988). Since models maximizing these alternative currencies often make similar predictions regarding the amount of time spent in a food patch (Welham and Ydenberg 1988) or the amount of food collected (Carlson and Moreno 1982; Kacelnik 1984), it can be difficult to distinguish between the alternatives. Predicted optimal flight speeds, however, are quantitatively different for the two currencies and change in different ways in response to variation in foraging conditions (Welham and Ydenberg 1988).

In a previous analysis (McLaughlin and Montgomerie 1985), we quantitatively compared the flight speeds of female Lapland longspurs (Calcarius lapponicus) feeding their nestlings in the high arctic with three predicted flight speeds from models optimizing different currencies: the speed minimizing the rate of energy expenditure during flight (Vmp), the speed maximizing the distance travelled per unit energy expended (Vmr), and the speed maximizing the net rate of energy delivery to the nest.
Longspur flight speeds were consistent with the predicted values of $V_{ms}$ under a variety of wind conditions, but were significantly higher than predicted values of $V_{mp}$ and significantly lower than predicted values of $V_N$. Hence, parent longspurs appeared to fly at speeds that would minimize their travel costs for a foraging flight.

In that analysis, we considered only trips to foraging sites $\geq 50$ m from the nest. Longspurs flew slower on trips covering $<50$ m, suggesting that acceleration costs had a significant effect on the speeds used for shorter flights. Since our investigation, Houston (1986) has developed models that incorporate an energetic cost for acceleration (i.e., takeoff). These models predict how the optimal flight speeds change with increases in the travel distance between the nest and foraging sites.

In this paper, we compare the flight speeds used by foraging longspurs with the speed maximizing the overall rate of energy delivery to nestlings ($V_Y$) and the speed maximizing the distance travelled per unit energy expended ($V_{ms}$). This study differs from our earlier analysis (i) by testing the predictions of the models that incorporate a cost for acceleration and (ii) by focusing on the relationship between average flight speed and travel distance. Our previous study considered the relationship between flight speed and wind speed but excluded all flights shorter than $50$ m and was therefore based on a sample of only 25 flights made by four females. The analysis presented in this paper includes data for an additional 275 foraging trips and seven additional females.

**Methods**

**Field site and data collection**

Flight speed data were collected during the 1981 and 1982 breeding seasons (June and July) on the upland high arctic tundra at Sarcap Lake, Melville Peninsula, Northwest Territories (68°33′N, 83°19′W; see Montgomerie et al. 1983). Lapland longspurs were a common breeding bird at this site, with 10–23 territories/km$^2$. Montgomerie et al. (1983). Lapland longspurs were a common breeding bird at this site, with 10–23 territories/km$^2$. We collected data for 300 foraging trips made by 11 female longspurs, 7 observed in 1981 and 4 in 1982. Female longspurs typically flew low over the tundra from their nest to a foraging site where they collected food on the ground. Their entire foraging bout was easy to observe and quantify on the open tundra. We focused on females because they usually made more foraging trips per day than males, and they were easier to follow, usually visiting only one feeding site per trip.

Data were collected throughout the 8- to 9-d nestling period. Each female was observed for 0.5 h at a time in 1981 and 1 h at a time in 1982, from vantage points 20–50 m from the nest. During each observation period, we measured the time (±0.1 s) taken for a female to fly from her nest to a foraging site. Travel distance (±10%) and direction (to the nearest 22.5°) were measured with the aid of coloured flags placed on the breeding territories. In 1981 these flags were 50 m apart and arranged as transects extending 150 m away from the nest in the four cardinal directions. In 1982, we used a $240 \times 240$ m grid of flags, 30 m apart and centred on the nest. In general, we tried to watch each female for at least one observation period a day in 1981 and at least once every other day in 1982. Less than 5% of the foraging flights went beyond our grid markers and these were not included in our analyses.

**Terminology**

Air speed is the speed of the bird relative to the air, while ground speed is the speed of the bird relative to the ground. The speed of the air relative to the ground is called wind speed. Thus, a bird’s ground speed represents the vector sum of its air speed and the speed of the wind. In a head wind the windspeed vector is negative, while in a tail wind it is positive. The wind speed vector in the same direction as the bird’s air speed vector is called the following component of the wind. We concentrate on ground speeds in this study because they can be quantified without accurate measurement of wind speed. Average ground speed for a trip was calculated by dividing the distance travelled from takeoff (at the nest) to landing (at a foraging site) by the total time for the flight. We assume that after takeoff a female quickly accelerates to a constant speed, maintains that speed until she reaches a foraging site, then decelerates quickly to land. Field observations suggest that this is a reasonable assumption. The average speed therefore includes periods of acceleration and deceleration and will be slightly slower than the speed in midflight.

**Currencies**

For birds flying from place to place, the optimal speed is thought to be $V_{ms}$, the speed minimizing the cost per unit distance travelled, and hence the total cost of the trip (Tucker 1974; Rayner 1979). Some studies have found that birds fly at or close to this speed (e.g., Schnell and Hellack 1979; but see Gill 1985). For a foraging bird or bird feeding nestlings, however, $V_{ms}$ does not maximize the rate of energy gain and may not, therefore, be the speed that maximizes a parent’s reproductive success (Norberg 1981; Pyke 1981; Houston 1986).

In his food-delivery-rate models, Houston (1986) focuses on two different currencies. The first, called the overall rate of food delivery ($V_Y$), considers a parent bird that flies to a feeding site, feeds itself to recover its flight costs, and then collects a load of food for its nestlings. In this case, the optimal flight speed ($V_Y$) depends upon the rate ($G$) at which the bird collects energy from the environment (Houston 1986). The second currency is the net rate of energy gain ($N$). In this case the parent does not feed itself during the foraging trip, so its travel costs are subtracted from the energetic value of the food load collected for the offspring. In this case the optimal speed ($V_N$) depends specifically on the shape of parent’s food-loading curve (Houston 1986). The speed maximizing the overall rate of energy delivery to the nest ($V_Y$) is greater than the speed maximizing the net rate of energy gain ($V_N$).

It is difficult to determine which of these two delivery rate currencies is most appropriate for parent birds because adults may feed themselves on some trips and not others. Two female longspurs, for example, fed themselves on at least 56% (27/48) and 63% (12/19) of their foraging trips, respectively. We assume in this analysis that longspur parents usually feed themselves on each foraging trip to recover their own foraging and travel costs, so we contrast $V_Y$ with $V_{ms}$. The implications of travelling at $V_Y$ are considered in the Discussion.

**Data analysis**

We analyzed only outbound flights in a straight line that resulted in food being returned to the nest. Food carried in the bill during return flights might cause additional drag on the flying bird. Most important, our distance measurements were not as accurate for return trips, since females did not always fly directly back to the nest, but to sites up to several metres away, and then walked the remaining distance.

The flight speeds used by longspurs are affected by wind conditions (McLaughlin and Montgomerie 1985), and we do not have wind speed measurements for the majority of foraging flights analyzed here. For our main analysis, we grouped observed travel distances into fourteen 10-m intervals ranging from 10 to 149 m, and for each interval, calculated a median ground speed for each female. By using these median values we reduce the effects of pseudoreplication (see Hurlbert 1984) and we reduce the variation in recorded flight speeds due to varying wind conditions. We separately analyzed the air speeds calculated from 62 flights for which wind speed and direction were measured at eye level using a hand-held anemometer (see McLaughlin and Montgomerie 1985 for details).

**Predicted flight speeds**

Optimal speeds were calculated here using the same general methods and parameter values as in our previous analysis (McLaughlin and Montgomerie 1985). The energetic cost for steady-state flight (i.e., no acceleration) was estimated using Tucker (1974; his eqs. 2 and 5 combined):

\[
P(V) = 1.115[87.52 \rho^{-1} b^{-2} V^{-1} + 1.45 \rho^{0.5} \mu^{0.5} V^{-2.5} m^{0.66} (1 + 471.7 m^{-0.167} \rho^{-0.5} V^{-0.5} \mu^{0.5}) + 6.15 m^{0.724}]
\]
The energetic cost, \( E(V) \), of accelerating to speed \( V \) was estimated as the associated kinetic energy (see Houston 1986), where

\[
E(V) = \frac{0.5 m V^2}{b} \quad \frac{1}{2}
\]

For flights of distance \( D \), the cost of transport \( CT(V) \) (including acceleration costs) becomes

\[
CT(V) = \frac{P(V)}{V} + \frac{E(V)}{D}
\]

\( V_{me} \) is the speed that minimizes this cost \((\text{in } J/m)\) and thus maximizes the distance travelled per unit energy expended. It is found by taking the derivative of eq. 3 with respect to velocity and setting it equal to 0. Because this derivative is complex, values of \( V_{me} \) for trips of varying distance were calculated by numerical iteration.

As in our previous study, we used 0.028 kg as the body mass of a longspur. Wingspan was estimated as 0.294 m, using the equation for Passeriformes in Table 4 of Rayner (1979). Both air density and air viscosity were calculated from equations in Tracy et al. (1978), using the elevation at Sarcepa Lake (185 m) and the average ambient temperature \((10°C)\) measured during the study.

The speed maximizing the overall rate of energy delivery to the nest depends on the parent’s rate of energy collection at a foraging site \( (G, \text{in} J/s) \). We used Custer’s (1974) time–energy budget for a female longspur to estimate \( G \). For each day of the nesting period, we calculated the total energy requirements \((\text{in} J)\) for a female longspur and half her brood and divided this by the time \((\text{in} s)\) a female spent on the ground foraging per day. This provided a gross gain rate \((\text{in} J/s)\) while foraging. From this, we subtracted the costs incurred by a female while walking on the ground collecting food, assumed to be four times the basal metabolic rate \((\text{Custer 1974})\).

Calculated values of \( G \) ranged from 6.0 to 12.4 J/s. To ensure that we made the most conservative predictions of \( V_Y \) relative to \( V_{me} \) we used 6.0 J/s in our analysis. Predicted values of \( V_Y \) increase as the parent’s food collection rate \( (G) \) increases \((\text{Norberg 1981; Houston 1986})\). Thus, if longspurs were maximizing their overall rate of energy delivery to nestlings, we expected them to fly at least as fast as our predicted values for \( V_Y \).

Following Houston (1986), \( V_Y \) is the speed where

\[
G = \frac{V^2}{D} E'(V) + VP'(V) - P(V)
\]

Predicted values of \( V_Y \) from eq. 4 were also calculated by numerical iteration. When \( G = 0 \), then the optimal speed from eq. 4 is \( V_{me} \).

Food availability

To assess whether flight speeds changed in response to changing food abundance, we monitored the insect food available to longspurs in both 1981 and 1982. Insects were sampled using 0.1 to 1.0 m boards covered by plastic sheets coated with a sticky resin \((\text{Tanglefoot}®)\). Eight boards were used in 1981. The same 8 plus 12 additional sites were sampled in 1982. The boards were placed in all five of the main habitat types used by foraging longspurs. Insects were counted and classified by size and taxa every 4 d, at which point the resin-covered plastic was replaced. We report data for craneflies \((\text{Tipulidae})\) only here because they represent the major component of biomass in longspur diets during the nestling period \((\text{personal observation}; \text{see also Custer and Pitelka 1978})\).

Results

Direct tests

The average flight speeds used by female longspurs were greater on trips to feeding sites located farther from their nests \((r_s = 0.58, P < 0.0001, df = 80)\) in a fashion predicted by the models including an energetic cost for acceleration (Fig. 1). Thus, the energetic cost of acceleration should be considered when predicting the flight speeds of parent birds, especially when foraging flights cover short distances.

Predicted values of \( V_{me} \) relative to the ground were calculated for windless conditions, and for tail winds and head winds of 4 m/s. Sixty of the 62 foraging flights for which we measured wind speed were within this range of wind conditions. We therefore expected observed ground speeds to lie within this range of predicted values for \( V_{me} \) if females were maximizing the distance travelled per unit energy expended. It is clear that the median ground speeds of female longspurs were closer to the predicted values for \( V_{me} \) than to \( V_Y \) (Fig. 1); 73 of these speeds were within the range of values predicted for \( V_{me} \), while 6 were above that range and 3 were below. Predicted values for \( V_{me} \) tended to be slightly higher than observed median ground speeds on flights close to the nest and slightly lower on flights farther from the nest. As shown in Fig. 2, the majority (75%) of actual ground speeds recorded were within the predicted range of \( V_{me} \) and most (94%) of these observed speeds were well below \( V_Y \) even though our predicted values of \( V_Y \) were conservative (see Methods). In addition, predictions for \( V_Y \) on foraging trips greater than 110 m were greater than the estimated maximum sustainable speed for a longspur \((V_{max} = 13.2 \text{ m/s}; \text{Fig. 1}; \text{see McLaughlin and Montgomery 1985 for calculations})\).

To evaluate the two models further, we calculated \((\text{by iteration})\) the rate of energy gain at a feeding site \( (G) \) that minimized the sum of squared deviations (SS) between observed and predicted speeds. This technique is a variant of “inverse optimality” used by Kacelnik et al. (1986) to evaluate their two different currency models for foraging honeybees \((\text{Apis mellifera})\). The \( V_Y \) model predicted that \( G \) would be at least 6.1 J/s (eq. 4), while the \( V_{me} \) model predicted that \( G \) would be 0 J/s. Our estimate of \( G \) was 1.1 J/s (95% confidence limits: 0.7 and 1.5 J/s, respectively). Since \( G \) was significantly greater than 0 but much less than 6 J/s, neither model was entirely
appropriate, but the $V_{mr}$ model provided a better fit than the $V_Y$ model ($SS = 185$ vs. $661$, respectively). A value of $G > 0$ may indicate that longspurs were flying slightly faster than $V_{mr}$, or that there is some bias in the quantitative predictions of the $V_{mr}$ model.

In our earlier analysis (McLaughlin and Montgomerie 1985), we controlled for the effects of acceleration by considering only flights of $\geq 50$ m, and found that observed air speeds were most consistent with $V_{mr}$. The present analysis of ground speeds reaches the same conclusion, but our incorporation of an energetic cost for acceleration changes the predicted values for $V_{mr}$.

To re-examine our previous conclusion based on air speeds in light of the new predicted values that incorporate the cost of acceleration, we also analyzed 62 air speeds used by four birds for which we measured distance and direction travelled, as well as wind speed and direction. This analysis includes the 25 flights of 50 m or more analyzed in McLaughlin and Montgomerie (1985) plus 37 additional flights of $<50$ m. The effect of wind direction was taken into account by calculating the following component of the wind for each flight (see McLaughlin and Montgomerie 1985 for details).

When the effect of wind speed was controlled statistically using partial correlation analysis, we again found a positive correlation between average air speed and travel distance (partial $r = 0.57$, $P < 0.001$, df = 59). (Air speed and travel distance were both log-transformed to linearize the relationship between them.) This suggests that the cost of acceleration was also important in determining average air speeds and supports our previous conclusion with respect to ground speeds.

Also, for the 62 air speeds, the calculated value of $G$ that minimized the sum of squared deviations between observed and predicted air speeds was $1.2$ J/s (95% confidence limits: $0.4$ and $2.0$ J/s), almost identical to our estimate from the ground speed analysis. Thus, our various quantitative analyses based on both ground speeds and air speeds indicate that female longspurs fly at speeds closer to $V_{mr}$ than to $V_Y$.

![Fig. 2. Summary of observed ground speeds for 11 different female Lapland longspurs flying from their nest to a foraging site. Box plots shown here indicate the 10th, 25th, 50th, 75th, and 90th percentiles by horizontal lines as well as all data points outside this range. Sample sizes for each female are given above the figure. The shaded area indicates the range of predicted values for $V_{mr}$ calculated for winds with a following component of $\pm 4$ m/s. Arrows indicate predicted values for $V_{mr}$ and $V_Y$ in windless conditions. All predicted values shown are taken from Fig. 1 for flights of 57 m, the mean flight distance for all flights shown on this figure.](image)

![Fig. 3. Seasonal abundance of craneflies on the study area in 1981 and 1982. Mean numbers of craneflies trapped per sticky board during the previous 4-d period are plotted. Eight sites were sampled in 1981 and 20 in 1982. The histogram shows the total number of nestlings present in the 11 nests studied for each day during 1981 and 1982 combined.](image)

**Indirect tests**

Theory predicts that birds flying at $V_Y$ would increase their average speed when food is more abundant (Norberg 1981; Houston 1986), while birds flying at $V_{mr}$ would not change speed (see McLaughlin and Montgomerie 1985). We used two indirect tests to discriminate between these two qualitative predictions.

First, longspur offspring leave the nest just prior to the peak in insect (food) abundance (Fig. 3; see also Custer and Pitelka 1977). Thus, it is reasonable to assume that the rate of energy collection ($G$) at a foraging site increases during the nestling period. In support of this assumption we found that the overall rate of food delivery increases over this time period (unpublished data). The delivery rate model would predict that longspurs fly faster when nestlings are older, while the $V_{mr}$ model predicts no change. Using partial correlation analyses to control for the effect of travel distance, we found that only 1 of the 11 females displayed a significant positive correlation between average flight speed and nestling age. Overall, however, these analyses showed no support for a positive correlation between average flight speed and travel distance predicted by the $V_Y$ model (Fisher’s method of combining probabilities: $x^2 = 16.5$, df = 20, $P > 0.50$; see Sokal and Rohlf 1981, p. 780).

Second, insect abundances at Sarcpa Lake were much higher in 1982 than they were in 1981 (Fig. 3). Thus, if females were flying at $V_Y$ they would have flown faster in 1982 than they did in 1981, whereas there should have been no difference in average flight speed between these 2 years if longspurs flew at $V_{mr}$. To test these predictions we compared the relations between flight speed and travel distance (both variables log-transformed) for
the 2 years, using analysis of covariance. Longspurs increased their travel speed with increasing travel distance at similar rates in each year (comparison of slopes; \( F = 0.79, P > 0.30, \text{df} = 1.79 \)). The mean flight speeds (adjusted for variation in travel distance), 8.4 m/s in 1981 and 8.5 m/s in 1982, were not significantly different (comparison of adjusted means; \( F = 0.10, P > 0.75, \text{df} = 1.80 \)). Thus, longspurs did not fly faster when food was more abundant. Both of our indirect tests are consistent with the conclusion that females longspurs flew at \( V_{mr} \) rather than \( V_Y \) when feeding nestlings.

**Discussion**

**Longspurs fly at \( V_{mr} \)**

Our examination of the flight speed vs. travel distance relationship suggests that female longspurs flew at speeds closer to the speed maximizing the distance travelled per unit energy expended (\( V_{mr} \)) than the speed maximizing the overall rate of energy delivery to nestlings (\( V_Y \)). This result is consistent with our earlier study examining the relationship between flight speed and wind speed (McLaughlin and Montgomerie 1985).

There are various reasons why this conclusion should be robust. First, we used both air speeds and median ground speeds to test the alternative models, and both data sets support the \( V_{mr} \) model rather than the \( V_Y \) model. The advantage of the air-speed analysis is that it directly incorporates wind-speed effects while the ground-speed analysis does not. However, the ground-speed analysis is based on much larger samples of foraging flights and birds. Second, our two indirect tests examining the relationship between flight speed and food abundance are consistent with the conclusions of the direct, quantitative tests of the speed vs. travel distance relationship. This is important because the direct tests are based on only rough estimates of both the gain rate (\( G \)) and the various flight costs (eqs. 1 and 2). It is simply not known how accurate these estimates are for longspurs. The indirect tests do not require that these parameters be known (Norberg 1981).

Longspurs are also ideal birds for evaluating these two flight-speed models. Food is abundant on the arctic tundra (Fig. 3) and nestlings grow quickly (Maher 1964; Hussell 1972) so that a high rate of food collection and, therefore, substantially faster flight speeds are predicted by the \( V_Y \) model (Fig. 1). Large differences between the alternative optimal speeds facilitate our ability to discriminate between the two models.

We have not dealt with all of the possible currencies that female longspurs could optimize by adjusting their flight speed. For example, we have not considered the net rate of energy delivery to the nest (\( N \)) that is maximized by flying at \( V_Y \). Since our observations indicated that longspurs feed themselves on the majority of foraging trips, they could not (by definition) maximize the net rate of energy delivery to the nest on those trips (see Houston 1986). Further, observed flight speeds were not consistent with the \( V_N \) model, which also predicts that flight speed will be positively correlated with food abundance (Houston 1986). More information regarding the food-loading behaviour of parents at feeding sites is required before this alternative can be examined directly.

**Implications of flying at \( V_{mr} \)**

Our analyses indicate that female longspurs fly at speeds that minimize their travel costs for a foraging flight. Such behaviour is more consistent with maximizing foraging efficiency (the ratio of energy gained to energy spent), by reducing travel costs, than it is with maximizing the rate of energy delivery to nestlings. This finding differs from those of earlier studies of parent birds feeding nestlings which usually concluded that parents maximize their rate of energy delivery to the nest (e.g., Carlson and Moreno 1982). Many studies, however, have tested only the qualitative predictions of delivery rate models (Stephens and Krebs 1986). Few of these studies attempt to discriminate between efficiency and delivery rate (but see Carlson and Moreno 1982; Kacelnik 1984), and models optimizing these alternative currencies often make similar qualitative predictions. Other observations also suggest that parent longspurs attempt to reduce travel costs when looking after their chicks. The dispersal and division of broods after nest departure also result in decreased travel costs because of the multiple central place foraging routes used by parents at that time (see McLaughlin and Montgomerie 1989).

We conclude that longspur flight speeds are most consistent with the maximization of foraging efficiency. This suggests that the fitness gains associated with reducing energy costs (when flying at \( V_{mr} \)) are greater than the fitness gains accrued by saving time (when flying at \( V_Y \)) that can then be used for additional foraging. There are several ways this could arise. First, as discussed by McLaughlin and Montgomerie (1985), in years with good weather conditions parent longspurs probably have little difficulty meeting both their own daily energy requirements and those of their brood. In such years overall food abundance is high, and the birds could forage for up to 24 h in the continuous daylight. Under these conditions, increasing the rate of energy delivery to nestlings would not increase reproductive success. Second, flying at \( V_Y \) requires that parents have knowledge of their expected rate of energy collection at foraging sites (\( G \)). Because of the temporal and spatial variability in insect abundance (Fig. 3; unpublished data), the costs incurred by the parents in estimating \( G \) so that they could fly at \( V_Y \) may outweigh the costs of using \( V_{mr} \) as an alternative. We do not know the magnitude of such costs, but our calculations suggest that using \( V_{mr} \) over \( V_Y \) results in only a 3–5% reduction in the overall delivery rate. Third, by flying at the substantially faster \( V_Y \) parents may increase their food delivery rate in the short term, but this may result in associated physiological costs (e.g., decreased endurance or health) that would reduce a parent’s overall performance during the entire period of parental care. Finally, the additional foraging trips made by a parent maximizing its delivery rate may increase the risk of nest predation.

Welham and Ydenberg (1988) suggested that the foraging behaviour of ring-billed gulls (Larus delawarensis) was truly intermediate between the predictions made by net energy and efficiency maximization models. Our calculated values of \( G \) could be interpreted similarly but, since only approximations were used to estimate \( G \), we feel that such a conclusion could be premature. Moreover, our indirect tests examining whether flight speed changed with varying food abundance support the hypothesis that these birds flew at \( V_{mr} \).

Our studies of longspur flight behaviour show that parent longspurs adjust their flight speed in response to wind speed (McLaughlin and Montgomerie 1985) and expected travel distance, but not with food abundance (this study). Further, longspur flight speeds are more consistent with a strategy of maximizing foraging efficiency than with maximizing the rate of energy delivery to nestlings. Models assuming that foragers maximize their delivery rate have made many successful predictions, but it is becoming clear that under some conditions an animal’s foraging strategy can deviate from this optimum and resemble efficiency maximization (Houston et al. 1988).
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